JOURNAL
OF THE
FISHERIES RESEARCH BOARD OF CANADA

[illegible] 26, N[illegible] March 1969

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JOURNAL OF THE FISHERIES RESEARCH BOARD OF CANADA

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The publication of the *Journal*, together with its predecessors, has been continuous since 1901. Its predecessors are *Contributions to Canadian Biology* published from 1901 to 1925, *Contributions to Canadian Biology and Fisheries* from 1926 to 1934, and the *Journal of the Biological Board of Canada* from 1934 to 1937.

The *Journal* is published in annual volumes of twelve issues. This issue (Vol. 26, No. 3) was published March 31, 1969.

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All Fisheries Research Board of Canada publications are for sale by the Queen's Printer, Ottawa. Remittances must be in advance, payable in Canadian funds to the order of the Receiver General of Canada. Subscription rates to the *Journal* are: Canada, United States, Mexico, $9.50, single issue $1.00; to other countries, $1[illegible]5 and $1.25.

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Effects of Size-Selective Mortality and Sampling Bias on Estimates of Growth, Mortality, Production, and Yield

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RICKER, W. E. 1969. *Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production, and yield.* J. Fish. Res. Bd. Canada 26: 479–541.

Size-selective mortality decreases or increases the actual and back-calculated lengths of an age-group, while at the same time altering the shape and variance of its length frequency distribution only slightly or not at all. An index of intensity of selection (r) can be calculated from the difference in computed length (d) between the penultimate annulus at age n and the terminal annulus at age n–1, together with the standard deviation in length (s); it is $r = 1.349d/s$, and represents the difference in mean instantaneous mortality rate between the two halves of the frequency distribution. Instantaneous rates of increase in weight can be computed from length data by multiplying the difference between the natural logarithms of length 1 year apart by the exponent in the weight–length relationship. When there is size-selective mortality, the difference between the rate (G_X) based on observed weights in successive years differs from the true rate (G) based on the terminal length differences computed from scales. Similarly the instantaneous rate of decrease in numbers (Z) differs from the rate of loss of weight or ponderal mortality rate (Z_W). It is found that $G - G_X = Z_W - Z$. "Lee's phenomenon" may be caused by selective mortality or by biassed sampling. Unlike selective mortality, biassed sampling produces only *positive* Lee's phenomenon (back-calculated lengths from older fish *less* than those calculated from younger fish), regardless of whether it is the smaller or the larger fish that are favoured by the sampling gear. The use of incorrect growth rates can lead to rather large errors in estimates of production of a stock. Errors in computation of yield, due to using numerical instead of ponderal mortality rates, tend to be much smaller.

Received November 22, 1968

INTRODUCTION

IN MOST OR PERHAPS ALL fish populations, the fish of each year-class are subject to differential mortality in relation to size, at some stage or other of their life. Except during the first year or two of life, this usually takes the form of greater mortality among larger individuals than among smaller ones of a given age. Size-selective mortality is associated with an effect that was first observed by Sund (1911),[1] was discussed in detail by Lee (1912) and by Lea (1913), and is commonly known as "Lee's phenomenon." In the growth histories of sprats, herring, haddock, and trout, as calculated from annual marks on their scales, these investigators observed that the fish taken at the older ages were increasingly those whose computed growth in earlier years was slow. Such observations constitute Lee's phenomenon, in the inclusive sense.

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[1] See Appendix I.

Printed in Canada

There is no need to review the extensive writings concerning the nature of Lee's phenomenon: good reviews are available by Graham (1929), Van Oosten (1929), Hile (1936), Bryuzgin (1963), and others. It was shown early that the possible causes are of three different types:

(1) *Technical* — Use of incorrect scale: body relationships in back-calculation of growth.

(2) *Biassed sampling* — Where fish of different sizes are not represented in samples of scales or otoliths in proportion to their abundance. Usually it is the smaller fish of an age-group that appear in samples less frequently than larger ones. The reason may be either that the sampling gear in use catches large fish more effectively, or the larger fish may have a different distribution or habits — often associated with the fact that more of them are mature and so take part in migrations or spawning maneuvers that make them more easily caught.

(3) *Selective mortality* — Where the mortality rate among the larger fish of an age-group is different from that among the smaller. Size-selective mortality may arise either from natural mortality factors, or (when fishing is a significant source of mortality in the population) from differing catchabilities of fish of different sizes.

Selective mortality, unlike the other two causes of Lee's phenomenon, is a property of the fish population rather than of technique. Most of what follows concerns its effects on estimates of the biological statistics of populations. Sampling bias will have to be considered, but only as a source of error — something that it is important to identify and, if possible, make adjustments for.

Methods of Back-Calculation of Growth

Before undertaking any interpretation of a particular example of Lee's phenomenon, it is necessary to be certain that a correct technique has been used to calculate fish size from annual marks on the scales or bones. Many methods have been suggested, most or all of which can give reliable results *in appropriate situations*. A recent good review and critique is by Bryuzgin (1963). Bryuzgin (1963), Shentyakova (1966a, b), and others have shown that different species, and different populations of the same species, can differ in respect to the shape or the parameters or both of the body: scale relationship (also body: otolith, etc.). This relationship may be straight, simply curved, or S-shaped. Its shape is likely to differ as between scales, otoliths, fin spines, etc., of the same group of fish. It may differ between scales from different sites on the fish's body, and between different measurements made on the same scale (Huntsman, 1918; Van Oosten, 1929). The kind of length measurement used (standard, fork, total, etc.) may also have some effect on the relationship obtained. Thus the kind of body: scale relationship must be determined for each population studied and each technique used.

In other words, for every new investigation it is necessary to fit a trend line empirically to a plot of body length against scale radius (or whatever structure is used), and use it as the basis for back-calculation. If the line indicated is straight and passes through the origin, lengths may be calculated by direct proportion (Lea's 1910 method). If it is straight but does not go through the origin, a slightly more complex calculation is necessary (Fraser's 1916 method). If the body: scale relationship is not linear, a parabolic or other curved line may be fitted mathematically (Sheriff's 1922 method); or the relationship may sometimes be straightened by transformation to logarithmic axes (Monastyrsky's 1926 method), preceded, where appropriate, by subtraction of a constant quantity (Fry's 1943 method). Finally, an empirical line may be fitted either freehand (Huntsman's 1919 method) or by running averages. For details see Chugunova (1959) or Tesch (1968).

All back-calculation methods, except the proportionality calculations, require that the annulus measurements as read from the scale be adjusted to terms of the average scale size for fish of the observed length, before applying the average body:scale relationship. This can readily be done numerically, but various mechanical devices have been devised to assist with the operation, starting with Huntsman's (1919) pivoted ruler and proceeding to the complex calculating boards and computing microscope stages proposed by Monastyrsky (1934), Fry (1943), Bryuzgin (1955), Kostarev (1967), and others.

There is today no reason to use incorrect back-calculation procedures, and in fact they appear to have practically disappeared. In this paper accurate back-calculation techniques will be assumed to be used throughout.

Example of Selective Mortality

Although hundreds of growth studies of fish have been published, it is difficult to find a completely satisfactory example to illustrate the whole range of effects of selective mortality. The principal reason is that in most studies sampling has not been carried back to age 1+,[2] or if it has, there is good reason to believe that it is not representative for the younger age-groups. An additional condition is, of course, that quite large samples at each age are necessary in order to keep sampling variability within bounds. Ideally, too, we should have representative samples *of the same year-class* in all years of its life.

Hile's (1936) data on an unfished population of ciscoes (*Coregonus artedii*) in Silver Lake, Wisconsin, are a satisfactory example in most respects. Samples were taken in 1928, 1930, and 1931 using a graded series of gillnets. Hile examines in detail the possibility of bias in sampling this population, and concludes that there is no appreciable bias in the average lengths of the various age-groups from age 2+ on up.[3]

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[2] In this paper "age 1+" refers to the interval between the time at which the fish becomes age 1 and that at which it becomes age 2, and so on. Also, the convention is used of beginning age 1+ at the start of a calendar year, even though this usually means that the fish will have lived for less than a full year during age 0+.

[3] Concerning age 1+ there was no completely satisfactory basis for an opinion, but these fish occurred in nets of two different mesh sizes, and their average length was only slightly larger in the larger mesh; hence sampling bias was probably not serious, and for our purposes it will be ignored.

In order to obtain as representative a picture as possible in Table 1 all the years represented in Hile's table 5 have been averaged, giving them equal weight regardless of the number of fish sampled. Exceptions are that two classes represented by a single fish have been disregarded, and I have used the interpolated value 85 mm for the age-1 length computed from age 3+ fish: the value quoted, 77.8 mm, is less than the figure calculated from age 4+ fish. To convert to an index of weight these average lengths (millimeters) were cubed[4] and divided by 10^5; this gives an arbitrary weight unit that will be called a gram for convenience. Natural logarithms of these weights were then taken, and the instantaneous rates of growth in weight were found by subtraction.

TABLE 1. Growth information for Silver Lake ciscoes. A: computed mean standard lengths in millimetres (L); B: $L^3/10^5$ ("grams"); C: $\log_e (L^3/10^5)$. Modified from Hile's data — see text.

Age at capture (*years*)	Length at capture (*mm*)		Computed size at scale annuli (*mm*)					
			1	2	3	4	5	6
		A	105.0					
1+	141	B	11.58					
		C	2.45					
		A	97.7	147				
2+	167	B	9.33	32.0				
		C	2.23	3.47				
		A	85.	133.	163.			
3+	174	B	6.14	23.4	43.5			
		C	1.81	3.15	3.77			
		A	79.0	128	154	172		
4+	180	B	4.93	20.8	36.3	50.6		
		C	1.60	3.04	3.59	3.92		
		A	76.7	120	146	165	181	
5+	188	B	4.51	17.4	31.0	44.7	59.0	
		C	1.51	2.86	3.43	3.80	4.08	
		A	75.0	116	138	160	177	190
6+	196	B	4.22	15.4	26.3	40.6	55.4	69.2
		C	1.44	2.73	3.27	3.70	4.04	4.24

In Fig. 1 the growth of the Silver Lake ciscoes is plotted in terms of length (A), weight (B), and logarithm of weight (C). Each ascending line in the

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[4] Hile (table 27) gives weight–length relationships for Silver Lake ciscoes in which the exponent of length is 3.32 for males and 3.45 for females. However, these are computed from fish in the length range from 130 to 204 mm only, and the equations yield questionable pairs of values if they are extrapolated to apply to the smaller fish included in Table 1. A relationship based on a wider range of fish sizes would probably have an exponent much closer to 3. In any event 3 is appropriate for the purpose of our illustration.

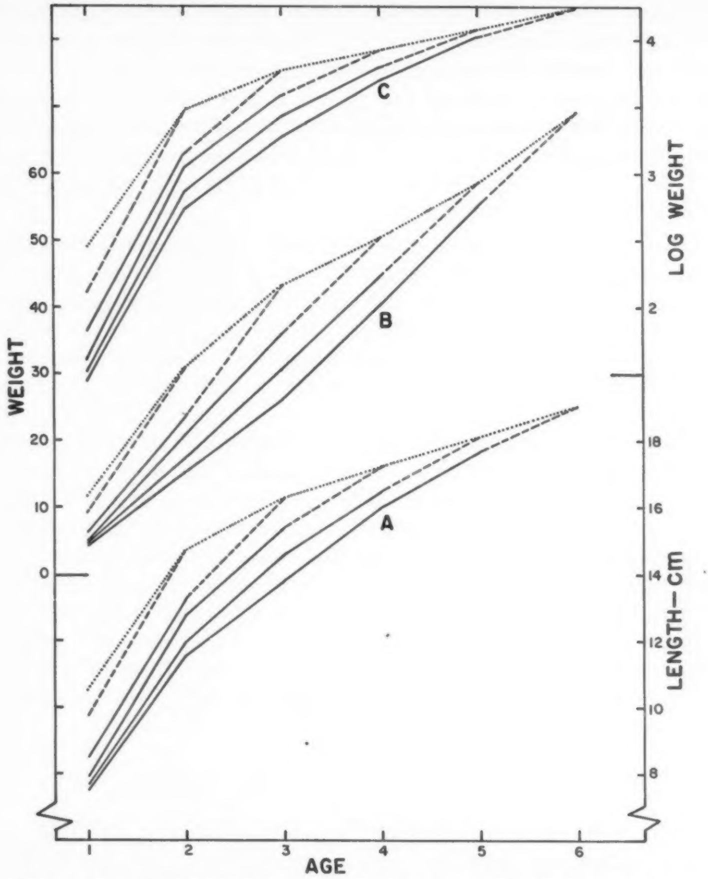

FIG. 1. Growth of Silver Lake ciscoes, from the data of Table 1. A — length; B — "weight" (length cubed); C — natural logarithm of weight. The dash segments of successive sample lines represent the true growth rate of the stock at successive ages. The dotted lines are the "X" growth rates.

figure represents the series of sizes computed from fish sampled at a particular age — from 1+ to 6+. These will be called *sample lines.*

The length graph (A) shows that the annual length increment declines throughout life, in all sample lines. There is some tendency for the different lines to diverge at ages 2–3, then come closer again at older ages.[5] The weight graph (B) of Fig. 1 shows that the absolute weight increment increases each year in all of the lines up to age 3 or 4, after which it remains rather steady. The plots of natural logarithms of weight (C in Fig. 1) give a picture of the instantaneous growth rates — these being equal to the slopes of the lines joining the points, or in other words the vertical distance between the points for successive ages.

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[5] Other growth series often show this effect more strongly. Zamakhaev (1964) says that this is the typical form of Lee's phenomenon, from which he distinguishes an atypical or "fan-shaped" form — first described by Kiselevich (1922) — in which the converging phase is lacking. However, there seems to be no fundamental difference between these two types: for some or all of the fan-shaped groups of curves it is likely that larger samples would have included fish of greater ages, in which convergence could appear.

MULTIPLICITY OF GROWTH RATES

Whenever selective mortality occurs, there will be several series of growth rates available, one for each sample line. If all ages are sampled up to age n, there are n–1 sample lines, so the number of growth rates available varies from 1 for the oldest age-group to n–1 for age 1+. In addition, another estimate of growth rate has often been used. This is obtained by comparing the weights of the surviving fish at each age, as indicated by the dotted line in Fig. 1.

Some practical problems immediately arise. Which of these growth rates is the best? Or is any one best for all purposes? Should some combination of them be used, and if so what? The analysis to follow was prompted by questions like these, and by curiosity concerning the quantitative effects of using incorrect growth rates in various types of computations. One such situation occurs when we are computing the effect of different rates of fishing, or of different ages or sizes at first capture, upon the yield obtained per unit weight of young stock (Ricker, 1945). At times changes in fishing regulations have been proposed on the basis of predicted gains of as little as 10%, so that even a fairly minor change in the statistics or approximations used might be important.

SELECTIVE MORTALITY AND LENGTH OF A YEAR-CLASS

SHAPE AND VARIANCE OF THE LENGTH FREQUENCY DISTRIBUTION

Where differential mortality exists, the calculated average length of a particular year-class in an earlier year of its life represents the former size *of the fish that survive to the sampling age*, but it differs from the average length of the year-class as it actually existed in times gone by. Jones (1958) has dealt with the problem of *how great* differential mortality must be in order to produce a given shift in length, and vice versa.

Consider a year-class of fish which does not grow at all, which has a normal (Gaussian) length distribution at the first age under consideration, and within which instantaneous mortality rate is a positive linear function of length. Jones shows that under these circumstances the average size of fish in the year-class becomes less as time passes, but *the frequency distribution of the lengths of the fish in the year-class remains normal, and their standard deviation does not change.*

There may be some besides myself who have found this hard to believe. "Common-sense" reasoning seems to suggest that, if the larger fish in a brood are being selectively removed, the frequency distribution of the survivors should become progressively skewed and its standard deviation should become progressively less. However, Jones's algebra can be verified by numerical computations, as shown in Fig. 2. Curve A is based on areas under the normal frequency distribution (from table 8.6 of Snedecor, 1946) plotted at the mid-points of intervals half a standard deviation broad (Table 2). For convenience the mean is taken to be 100 mm, and the standard deviation 10 mm.[6] Curve B represents the survivors after a year in which instantaneous mortality rate ranged from 0 to 1.5 (mean 0.75), increasing by 0.1 for each 5-mm increase in initial length (column 3 of Table 2). Curves C–F were obtained from A in the same way, but with increases of 0.2, 0.3, 0.4, and 0.5 per 5-mm interval, respectively, the average initial mortality rates being 1.5, 2.25, 3.0, and 3.75. The mean of the distribution is shifted to the left each time, but it is easy to see that the symmetrical shape and general range of variation is conserved.

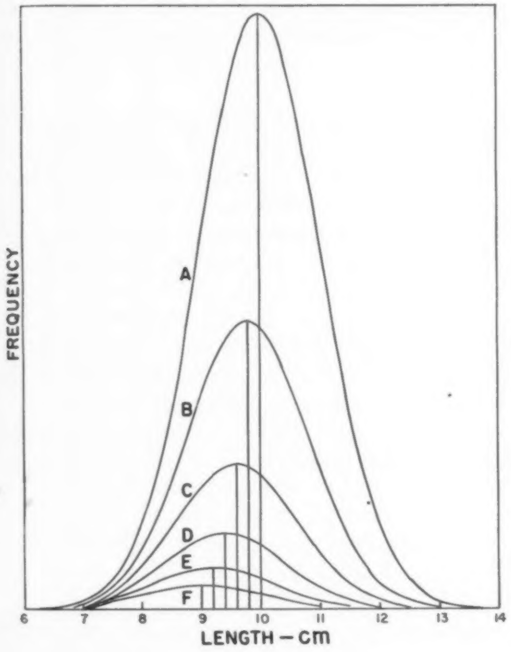

FIG. 2. Model A: Curves of length distribution at successive ages when there is a positive selective mortality at all ages of $a = 0.02$ per millimetre.

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[6] This is the population standard deviation from which the series was derived. The actual sample standard deviation computed from column 5 of Table 2 is $s = 10.10$ mm, but when Sheppard's adjustment for grouping $(5^2/12)$ is subtracted from the calculated variance the latter is reduced to 100.0 and the standard deviation to $s = 10.00$. In the computations to follow the population value $s = 10$ is used except where comparisons are being made with other calculated sample values.

TABLE 2. Model A: Decrease in numbers of a stock of 10,000 fish from age 1 to age 7, when they have a normal frequency distribution with standard deviation of 10 mm and the mortality rates shown in column 3 are maintained throughout life. In this and later tables, computations have usually been performed using more figures than are tabulated. Consequently, the totals shown often differ slightly from the actual sum of the items in a column, but they are the more accurate values. See Table 3 for more terminal figures in the "totals" row.

1 Length range (*mm*)	2 Mid-class weight (*g*)	3 Mortality rate (Z)	4 Survival rate (S)	5	6	7	8	9	10	11
				No. of fish in each length range at successive ages						
				1	2	3	4	5	6	7
60–65	2.44	0	1.0000	2	2	2	2	2	2	2
65–70	3.08	0.1	0.9048	11	10	9	8	7	7	6
70–75	3.81	0.2	0.8187	49	40	33	27	22	18	15
75–80	4.65	0.3	0.7408	166	123	91	67	50	37	27
80–85	5.62	0.4	0.6703	440	295	198	133	89	60	40
85–90	6.70	0.5	0.6065	919	557	338	205	124	75	46
90–95	7.91	0.6	0.5488	1498	822	451	248	136	75	41
95–100	9.27	0.7	0.4966	1915	951	472	235	116	58	29
100–105	10.77	0.8	0.4493	1915	860	387	174	78	35	16
105–110	12.42	0.9	0.4066	1498	609	248	101	41	17	7
110–115	14.24	1.0	0.3679	919	338	124	46	17	6	2
115–120	16.22	1.1	0.3329	440	146	49	16	5	2	1
120–125	18.38	1.2	0.3011	166	50	15	5	1	0	0
125–130	20.73	1.3	0.2725	49	13	4	1	0	0	0
130–135	23.26	1.4	0.2466	11	3	1	0	0	0	0
135–140	26.00	1.5	0.2231	2	0	0	0	0	0	0
Totals				10000	4821	2421	1266	690	391	231
Mean length (*mm*):										
Calculated from the frequency distribution				100.00	97.96	95.92	93.89	91.86	89.84	87.84
Computed from expression 1				100.00	98.00	96.00	94.00	92.00	90.00	88.00
Mean weight (*g*):										
Calculated from Pienaar's formula				10.300	9.706	9.135	8.588	8.063	7.560	7.078
Corresponding to computed mean length				10.000	9.412	8.847	8.306	7.787	7.290	6.815

CHANGE IN MEAN LENGTH

Still considering a population of fish that do not grow, the curves A–F in Fig. 2 can be regarded either as illustrating the application of different mortality rates within a single year, or as the progressive change in length distribution that results from applying the same mortality rates each year for 5 years. The latter situation is implied in the headings of Table 2, which gives the numbers in each length-class each year.

Jones (1958) also showed that the amount of shift in the mean size of an age-group is related to the rate of increase in instantaneous mortality rate within the group by the expression:

$$d = as^2 \tag{1}$$

where d = decrease in mean length of the fish in 1 year; a = the difference in instantaneous mortality rate, during this year, between fish that differ in size by 1 unit of length; s = standard deviation in length.

Fish such as are postulated above, that do not grow at all, would of course be very unusual. However, if the fish in a year-class do grow, then expression 1 can be used to compute the expected mean size of the fish at any age n, *as it is reconstructed by back-calculation from a representative sample of age* $(n+1)$. The exact pattern of growth makes no difference, except that if the group becomes more variable in length, the change in mortality rate per unit of initial length becomes less to compensate for it.

For example, suppose curve A in Fig. 2 represents the size distribution of age-1 fish (mean = 100 mm, s = 10 mm). A year later the year-class is sampled at age 2 and its size at age 1 is obtained by back-calculation. The standard deviation of these calculated lengths should be 10 mm; what will be their mean ? For insertion in expression 1 we have a = 0.02 (since mortality rate increases by 0.1 per 5 mm within the age-group), and s^2 = 100; hence:

$$d = 0.02 \times 100 = 2 \text{ mm}.$$

This is in fact the distance between the means of the calculated curves A and B in Fig. 2.

Expression 1 can of course also be used to calculate a when d is known, which is the more common situation. Trial calculations indicate that, generally speaking, it takes a rather large selective mortality to produce a rather small shift in mean length, as shown by the computed values of a given below:

Standard deviation in length (s, in *mm*)	Increase (a) in mortality rate, per mm of within-age-group increase in length, that is required to produce a difference (d) between true length and back-calculated length of the magnitude shown			
	d = 2 mm	d = 5 mm	d = 10 mm	d = 20 mm
5	a = 0.08	a = 0.2	a = 0.4	a = 0.8
10	0.02	0.05	0.1	0.2
20	0.005	0.0125	0.025	0.05
50	0.0008	0.002	0.004	0.008
100	0.0002	0.0005	0.001	0.002

In practice, an a-value from expression 1 must be regarded as a somewhat artificial quantitative measure of selectivity, but one that is quite adequate for orientation and comparative purposes. Jones's assumption that the increase in instantaneous mortality rate with length is linear has of course not been tested against actual observations, and indeed to obtain mortality data in the necessary detail would be extremely difficult. It is also true that many distributions of fish lengths at a given age deviate somewhat from normal. However, calculations of frequency distributions using moderately curved selection relationships show only minor differences from those using the best (weighted) linear fit to the same curve, and moderate departures from normality also make little difference. Hence it is legitimate to use this model provided we don't strain it into unsuitable applications. For example, frequencies computed from it are not likely to be realistic at distances more than 1.5 or so standard deviations from the mean, so it should *not* be used to calculate the life expectancies of fish in the tails of the frequency distribution.

INDEX OF INTENSITY OF SELECTION

It will be useful also to have a standard unit of selectivity that is independent of the mean size and variability in size of an age-group. Continuing with Jones's postulates (normal length distribution and linear change in instantaneous mortality rate with length within an age-group), an *index of intensity of selection* (r) or selectivity index may be defined as:

$$r = 1.349as = 1.349d/s \qquad (2).$$

This is the difference in instantaneous mortality rate between fish that lie one probable error ($0.6745s$) on either side of the mean of the age-group, provided of course that the whole of the group lies within the length range in which mortality increases linearly. Under these circumstances *the selectivity index* (r) *is equivalent to the difference in average instantaneous mortality rate between the smaller half and the larger half of the age-group.*

Because the selectivity index is independent of mean size, an age-group of minnows might have a value of r quite similar to an age-group of tunas, though the values of a would of course be very different. In the example of Table 2, $r = 0.27$ at all ages.

Expression 2 might also be used in reverse to compute a and d. For example, if returns from tagged fish in an age-group were divided into two halves at the mean size at tagging, r would be equal to the difference between the estimated instantaneous mortality rates of the two halves, and a could be calculated from expression 2.

SELECTIVE MORTALITY AND AVERAGE MORTALITY RATES

CHANGE IN AVERAGE MORTALITY RATE WITH AGE

Size-selective mortality means that the larger fish in a year-class disappear more rapidly than the smaller ones (or vice versa). Hence it is obvious that *if* there were no other factors making for change in mortality rate, the overall average mortality rate of the surviving fish would decrease with time — not only from year to year but also within each year.[7]

It is worthwhile to get some idea of the magnitude of this effect. As an example, assume that the curves in Fig. 2 represent the calculated 1st-year length frequency distributions of a year-class sampled in 6 successive years of its life, which we will refer to as population Model A. The initial mean instantaneous mortality rate is 0.75 per year, increasing from 0 in the 60–65 mm range to 1.5 in the 135–140 mm range (Table 2); and these rates continue to characterize fish of the respective initial lengths throughout their life. Column 3 of Table 3 shows the mean mortality rate at the start of successive years. The amount of decline in average mortality rate caused by the selective mortality is almost constant, decreasing only at older ages. Its initial value is 0.0408; in terms of the variables of expressions 1 and 2 this is equal to $0.204as$, or $0.151r$.

Columns 5 and 6 of Table 3 show the average mortality and survival rates *within* successive years, for the same population. Average rates are of course what would be directly measured by most available methods, such as age frequencies in samples, tag returns, and so on.

TABLE 3. Model A: Mean mortality and survival rates for the stock of Table 2 and Fig. 2. Columns 2, 5, and 6 are from the totals at the foot of Table 2, and 3 and 4 are weighted values computed from the distribution of mortality with respect to length and weight.

1	2	3	4	5	6
		Instantaneous mortality rate at start of year		Avg numerical mortality and survival within the year	
Age	No. of fish N	Numerical Z	Ponderal Z_W	Mortality Z	Survival S
1	10000	0.7500	0.8100	0.7296	0.4821
2	4821.02	0.7092	–	0.6888	0.5022
3	2421.00	0.6684	–	0.6481	0.5231
4	1266.33	0.6277	–	0.6074	0.5448
5	689.85	0.5871	–	0.5669	0.5673
6	391.33	0.5468	–	0.5267	0.5906
7	231.10	0.5067	–		

---

[7] For lack of better information, biologists frequently postulate an average population mortality rate that does not change with age, in making numerical population models. However, when there is positive differential mortality by size, such an assumption implies that the mortality rate of the fish *of any particular initial size* must gradually increase!

Numerical and Ponderal Mortality Rates

Estimates of mortality rate have heretofore always been made in terms of *numbers* of fish dying. But if mortality is greater among the larger fish, the rate of loss of biomass due to mortality will be greater than the rate of loss of numbers, because more of the larger ones perish. Let us define a *ponderal survival rate* (S_W) as the biomass of the survivors of a brood after 1 year, divided by the biomass that the brood would have achieved if all of its members had lived (and growth rate were unaffected by abundance). The instantaneous *ponderal mortality rate* (Z_W) will then be defined as the natural logarithm of the ponderal survival rate (with sign changed).

In Model A the mean ponderal mortality rate at the start of year 1 can be calculated from the expression:

$$Z_W = \Sigma(N_i W_i Z_i)/\Sigma(N_i W_i)$$

where, for each length-class, N_i is the number of fish present, W_i is the mid-class weight of the fish, and Z_i is the instantaneous mortality rate in numbers. Its value is $Z_W = 0.8100$ (column 4 of Table 3). As expected, it is larger than the numerical mortality rate Z, the difference being 0.060 or 8%. To obtain Z_W in subsequent years it would be necessary to postulate in detail the rate of growth of the fish in each original length-class of Table 2, throughout their life, so that their actual weight could be computed in successive years.

We might also extrapolate slightly and say that the average value of Z_W *during* the 1st year of Table 3 is close to $0.8100–0.0204 = 0.7896$, because 0.0204 is the difference between the initial and the average numerical mortality rates.

RELATIONSHIPS BETWEEN GROWTH RATES AND MORTALITY RATES

Population Model A

The frequency distributions B–F of Fig. 2 and Table 2 represent the back-calculated lengths at age 1 of fish sampled at successively older ages, for the Model A situation where selective mortality continues at a constant rate throughout life. In order to add a fairly realistic growth component, we may notice that in Fig. 1C the slopes of the different lines within individual years of life do not differ much, and they have no consistent trend. Hence in our model we will apply the same instantaneous rate of increase in weight to the fish of all of the sample lines in the appropriate years, as follows:

Year	Instantaneous growth rate
1+	1.5
2+	0.5
3+	0.4
4+	0.3
5+	0.2
6+	0.15

The construction is shown in Table 4. It starts from the calculated true mid-class mean lengths in centimetres (L), shown in the A rows of column 3; the weight in grams corresponding to these is taken as equal to $0.01L^3$ (B rows in column 3),[8] where $b = 3$ is the exponent in the weight–length relationship $W = aL^b$. From these the natural logarithms of weight are obtained (C rows in column 3). To each of the C values in column 3 the successive growth rates listed above are added, and from these the corresponding mean weights and

TABLE 4. Model A: Growth in a fish population characterized by 2 mm of selective-mortality Lee's phenomenon at age 1 between all sample lines, and the same mean instantaneous rate of increase in weight for fish of all sample lines at each age. A: mean length of the fish in centimeters; B: mean weight in grams; C: natural logarithm of weight.

1	2	3	4	5	6	7	8
Age at capture		Size at age					
		1	2	3	4	5	6
1	A	10.0					
	B	10.0					
	C	2.3026					
2	A	9.8	16.16				
	B	9.412	42.18				
	C	2.2420	3.7420				
3	A	9.6	15.83	18.70			
	B	8.847	39.65	65.43			
	C	2.1802	3.6802	4.1802			
4	A	9.4	15.50	18.31	20.93		
	B	8.306	37.23	61.43	91.55		
	C	2.1169	3.6169	4.1169	4.5169		
5	A	9.2	15.17	17.92	20.48	22.62	
	B	7.784	34.88	57.52	85.83	116.0	
	C	2.0524	3.5524	4.0524	4.4524	4.7524	
6	A	9.0	14.84	17.53	20.03	21.99	23.66
	B	7.290	32.67	53.87	80.36	106.3	132.5
	C	1.9865	3.4865	3.9865	4.3865	4.6865	4.8865

---

[8] L. V. Pienaar has developed an expression for calculating the true average weights of the fish in each year-class from the weight–length relation for individual fish and the standard deviation in length (Pienaar and Ricker, 1968). In Model A the true weights at age 1 are 3.0–3.7% larger than those corresponding to the mid-class length, as shown in the last two lines of Table 2; at older ages the differences might be somewhat greater (depending on the variability in length at each age). Another approach is to compute a weight–length relationship from mean W and mean L for entire age-groups; this yields the "year-class *b*" of Ricker (1958), which can be used in expressions 4 and 6 below. However the approximation used here is accurate enough for our purposes, particularly since only the ratios of the weights will be used.

lengths are computed (B and A values in columns 4–8). The whole is plotted in Fig. 3.

If Table 4 was obtained by observation, the order would be reversed: all the A lines would first be obtained by back-calculation from samples taken at successive ages, and from these the weights and their natural logarithms would be computed. The differences of logarithms then become the estimated instantaneous growth rates.

Notice that if weights are being considered as proportional to some known exponent of length, as here, then it is not necessary to actually compute them. The natural logarithms of the lengths at the start and end of a year are found and the difference is multiplied by the appropriate exponent in the weight–

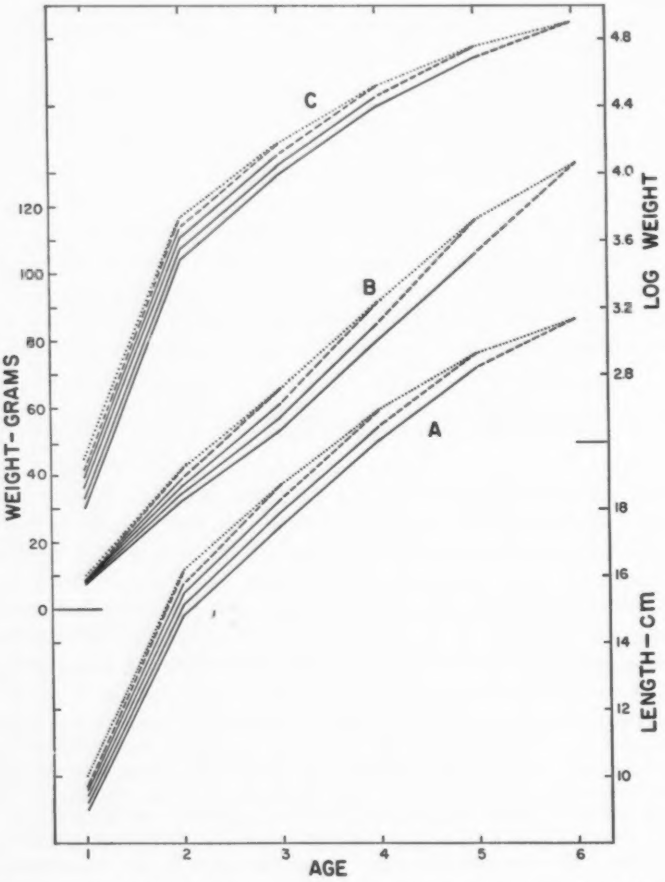

FIG. 3. Model A: Growth curves for successive sample lines. Symbols as in Fig. 1.

length relationship to obtain the instantaneous rate of increase in weight, as in expression 4 below.

TRUE GROWTH RATES AND "X" GROWTH RATES

Still considering Table 4, and treating it now as if it were a body of experimental data, the most recent and most direct information on the rate of growth of the surviving fish of a year-class in successive years is that indicated by the final pair of entries in each line of the Table. This is represented by the dash terminal segment of each ascending line in Fig. 3. These, therefore, are the direct estimates of the growth of the year-class during successive years of its life.[9] The slopes of the dash lines in the C group of Fig. 3 are equivalent to the differences between the two right-hand entries in each C-line of Table 4, and are the instantaneous rates of increase in weight at each age. We will call these the *true instantaneous growth rates*, represented by the symbol G:

$$G = \log_e W_2 - \log_e W_{1C} \qquad (3).$$

Here W_2 represents the mean weight of the fish in a year-class at the end of its most recent complete growth year (as indicated by the last annulus on the scale, or the scale margin if growth for that year is completed), and W_{1C} is the calculated mean weight at the penultimate annulus on the same scale.

Since we are treating weight as proportional to the cube of mean length (L), expression 3 can also be written in the form:

$$G = 3\left[\log_e L_2 - \log_e L_{1C}\right] \qquad (4).$$

In many growth studies, however, back-calculations cannot be made, or else *are* not made, and growth is estimated by comparing the sizes of the surviving fish sampled at successive ages. These *"X"-type instantaneous growth rates* (G_X) are measured by the slopes of successive segments of the dotted line in Fig. 3C, and are equal to the differences between the right-hand entry for successive ages in the C lines of Table 4:

$$G_X = \log_e W_2 - \log_e W_1 \qquad (5).$$

The corresponding expression in terms of length is:

$$G_X = 3\left[\log_e L_2 - \log_e L_1\right] \qquad (6).$$

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[9] Yet even these may not be completely representative of growth during the year, because the growth rate measured is that of the fish that *survive* to the end of the year. If a greater proportion of the larger fish die during the year than of the smaller, the larger fish will contribute somewhat less than they should to the growth rate estimate for the year as a whole. Hence, insofar as larger fish differ in growth rate from smaller fish, the above estimate of growth for the year will be slightly biassed. However, this is a third-order effect that can be neglected for our purposes. In any event, it cannot be assumed that the fish which die, at any particular size, have had exactly the same growth rate as those of the same size that survive, so there is always an element of uncertainty about the strict representativeness of an observed growth rate, whether or not size-selective mortality is present.

Obviously the X-type rates have a consistent bias making them too small when considered as estimates of G. This is summarized below for the Model A stock:

	Growth rates		
Age	G	G_X	Difference $G-G_X$
1+	1.5	1.4394	0.0606
2+	0.5	0.4382	0.0618
3+	0.4	0.3367	0.0633
4+	0.3	0.2355	0.0645
5+	0.2	0.1341	0.0659
6+	0.15	0.0826	0.0674

As age increases the bias of G_X becomes slightly greater absolutely, and much greater relatively, being –45% at age 6+.

A third or "Y" estimate of growth rate has sometimes been used. It is obtained by averaging the computed lengths of all fish available at each age, regardless of the number sampled. Figure 3 shows that in general this will give an estimate that lies between the true and the X rates above, but usually closer to the true rate; though the exact value depends on the number of fish in each sample line. Greatest deviation from the true rate will occur among the oldest age categories. Because of this variable bias we need not consider Y estimates further, and there is no real need to use them.

Rate of Increase in Biomass

In a real investigation of a fish stock an effort would be made to obtain estimates of not only the pattern of growth shown in Table 4, but also of the actual or relative number of fish present at each age as shown in column 2 of Table 3. The product of number of fish (N) times their average weight (W) is of course the biomass (B) of the age-group in question. The quotient of two successive biomasses (B_2/B_1) is the factor representing the stock's increase or decrease during that year, and the difference of the natural logarithms of the biomasses is the instantaneous rate of increase in biomass (H), which may be positive or negative:

$$H = \log_e B_2 - \log_e B_1 = \log_e N_2 W_2 - \log_e N_1 W_1 \qquad (7).$$

Thus H is available by observation.

Now by definition the rate of increase in biomass is equal to the true growth rate (G) less the ponderal mortality rate (Z_W):

$$H = G - Z_W \qquad (8).$$

Hence computation of ponderal mortality rate presents no difficulty.

Expression 7 can be put in the form:

$$H = [\log_e W_2 - \log_e W_1] + [\log_e N_2 - \log_e N_1] \qquad (9)$$

which is the difference between the X growth rate and the numerical mortality rate:

$$H = G_X - Z \qquad (10).$$

Combining expressions 8 and 10:

$$G - G_X = Z_W - Z \qquad (11).$$

The X-type growth rate is evidently not a pure growth rate, but *is equal to the true growth rate reduced by the extra rate of loss of weight which occurs because causes of death are selective.*

As an example of these relationships, consider the first year of life of the Model A population (data are from Tables 3 and 4, but using more terminal digits). Here $N_2 = 4821.02$, $N_1 = 10{,}000$ even; $W_2 = 42.1814$ g, $W_1 = 10$ g even, $W_{1C} = 9.4119$ g. The numerical mortality rate is:

$$Z = -\log_e(4821.02/10{,}000) = 0.7296.$$

The biomass values are:

$$B_2 = 4821.02 \times 42.1814 \text{ g} = 203.357 \text{ kg}$$

$$B_1 = 10{,}000 \times 10 \text{ g} = 100 \text{ kg}.$$

From expression 7, the rate of increase of biomass is:

$$H = \log_e 203.357 - \log_e 100 = 0.7098.$$

From expression 3, the true rate of growth is:

$$G = \log_e 42.1814 - \log_e 9.4119 = 1.5000.$$

Hence from equation 8, the ponderal mortality rate is:

$$Z_W = 1.5000 - 0.7098 = 0.7902.$$

This is within 0.1% of the estimate $Z_W = 0.7896$ obtained by direct calculation and extrapolation from Tables 2 and 3 (p. 490 above).

Further, the X growth rate is, from equation 5:

$$G_X = \log_e 42.1814 - \log_e 10 = 1.4394$$

and the identity of expression 11 checks out as follows:

$$1.5000 - 1.4394 = 0.7902 - 0.7296.$$

SELECTIVE MORTALITY CAUSED BY GRADUAL RECRUITMENT TO A FISHERY

Recruitment of a year-class to a fishery, as the term is used here, means its increase in vulnerability to the fishing gear in use, as a result of increase in individual size, changed distribution, or changed behaviour. It is commonly assumed or implied that vulnerability reaches a plateau somewhere in the middle part of the length range of the population. When all the fish in a year-class have reached this size, they are said to be "fully recruited." Change in vulnerability among the larger fish is discussed later (p. 501).

Since, in general, fish become vulnerable to nets or hooks over a particular size range, rather than at a particular age, and since fish of a given age vary greatly in size, it is obvious that fishing during the recruitment period will normally be a cause of selective mortality within the age-groups concerned. The faster-growing fish become vulnerable first, and are selectively removed from the year-class until all its members become fully vulnerable. This cause of Lee's phenomenon has been discussed and emphasized by Thompson (1923), Smith (1956), and Jones (1958, 1960), among others.

Population Model B

To construct a numerical model of recruitment having complete verisimilitude would be a complex matter, but a number of simplifying approximations can be used, without any damaging loss of realism for our purposes. (1) Numerous experiments have indicated that vulnerability to a trawl, gillnet, or hook of a given size is usually related to fish length by an ogive (flat S-shaped curve), or by an ascending curve with an asymptote (cf. McCracken, 1963). However, usually much the greater part of either type of curve is well approximated by a straight line, so we will make little error by treating recruitment as a process in which instantaneous rate of fishing mortality increases linearly with the length of the fish, between fixed limits of course. (2) Another simplification will be to relate rate of fishing during a whole year to the size achieved at the start of the year. (3) A third simplifying assumption is that all fish of a given age (after reaching age 1) increase in length by the same absolute amount each year. To be more realistic the year-class's variability in length should be made to increase for 1 or 2 years, then decrease (see p. 506, below). However this departure from plausibility has little effect on the points being examined, and the calculated lengths at age 1 are not affected at all.

Model B starts out with the same normal length distribution as Model A (column 5 in Table 2), with a mean length of 100 mm and standard deviation of 10 mm. The procedure used is to compute the abundance, mean length, and mean weight of the fish in each half-centimetre length-class from age 1 through age 7, considering the fish to be concentrated at the midpoint of each class. The following parameters were used: *Length increase in successive years*: 1st — 50 mm; 2nd — 30 mm; 3rd — 30 mm; 4th — 20 mm; 5th — 20 mm; 6th — 15 mm; 7th — 15 mm. *Instantaneous natural mortality rate*: $M = 0.2$ for all ages and sizes. *Instantaneous rate of fishing*: $F = 0$ for length-classes 145–150 mm and less; $F = 0.1$ for length-class 150–155 mm, increasing by 0.1 for each 5-mm increase in length, up to $F = 1.3$ for length-class 210–215 mm and larger.

The following statistics were computed for each length-class at each age:

$Z = F + M$ — instantaneous total mortality rate during the year.
$S = e^{-Z}$ — survival rate.
$A = 1 - S$ — actual mortality rate.
N — number of fish at the start of the year.
$\bar{N} = NA/Z$ — average number of fish on hand during the year.
$F\bar{N}$ — catch in numbers.
L — the mid-class length at the start of the year, in millimeters.
$W = L^3 \times 10^{-5}$ — weight corresponding to mean length at the start of the year, in grams.
$G = \log_e(W_2/W_1) = 3(\log_e L_2 - \log_e L_1)$ — the instantaneous rate of the growth during the year. The subscripts 1 and 2 represent the beginning and end of a year. The difference between this expression and expression 4 above results from the fact that we are dealing with fish considered to be of uniform size; that is, no selective mortality is possible *within* a length-class.
$H = G - Z$ — instantaneous rate of increase of biomass.
$B = NW \times 10^{-3}$ — biomass at the start of the year, in kilograms.
$\bar{B} = B(e^H - 1)/H$ — average biomass present during a year.
$F\bar{B}$ — yield during the year.

The complete table showing these computations is quite extensive, but a summary is given in App. Table 1 of Appendix 2, and App. Table 2 shows the details of the calculation for 1 year. From the complete table the sums ΣN, $\Sigma\bar{N}$, $\Sigma(F\bar{N})$, ΣB, $\Sigma\bar{B}$, and $\Sigma(F\bar{B})$ were obtained, summed over all length-classes each year. Also the mean length, L, of the surviving stock at the beginning of each year was determined, and the corresponding weight W (taken as $L^3 \times 10^{-5}$).

CURRENT AND BACK-CALCULATED LENGTHS FROM REPRESENTATIVE SAMPLES

Consider the situation where a completely unbiassed sample of each age-group in Model B can be taken at the start of the year and back-calculations of growth are made from the scales. Assuming perfect technique, the lengths calculated for one year earlier (L_C) will be equivalent to the observed mean lengths obtained from the model (L), less the amount of growth for the previous year that is specified in the text above (p. 496). Lengths in earlier years can also be computed in the same way (Table 5).

Under these ideal circumstances Fig. 4 shows the length distribution of the year-class at the start of successive years. Recruitment to the fishery

TABLE 5. Model B: Computed sizes of fish taken by representative samples at the start of each year.

1	2	3	4	5	6	7	8
Age when sampled	Computed size at successive annuli (*mm*)						
	1	2	3	4	5	6	7
1	100.00						
2	100.00	150.00					
3	98.86	148.86	178.86				
4	96.99	146.99	176.99	206.99			
5	95.32	145.32	175.32	205.32	225.32		
6	94.90	144.90	174.90	204.90	224.90	244.90	
7	94.88	144.88	174.88	204.88	224.88	244.88	259.88
d	0	1.14	1.87	1.67	0.42	0.02	–

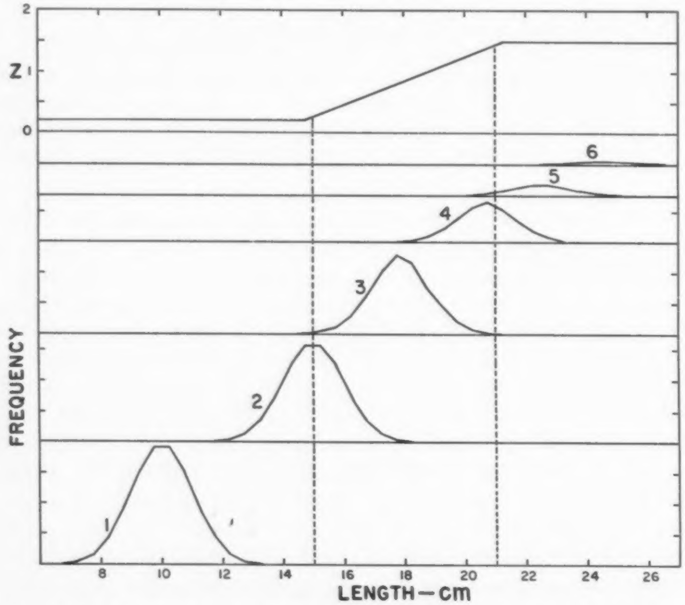

FIG. 4. Model B: Length frequencies in the stock at the start of successive years, and (*top panel*) the relation of total instantaneous mortality rate (Z) to length at the start of each year.

begins when the fish are age 2 and is practically complete at age 6, when all but the smallest length-class is fully vulnerable.

Back-calculated lengths at age 1 are shown as the series of "A" curves in Fig. 5. Curve 2A is symmetrical because there was no fishing between ages

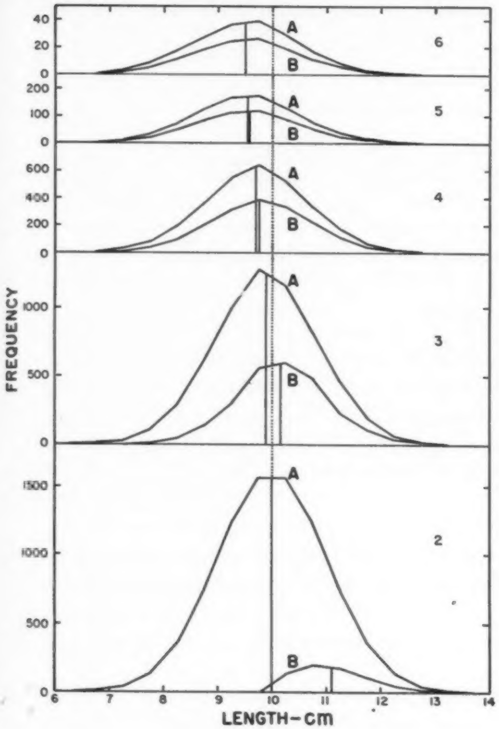

FIG. 5. Model B: Comparison of (A) age-1 length frequencies back-calculated from samples taken representatively from the whole age-group at the beginning of each year; and (B) age-1 length frequencies back-calculated from representative samples of the catch of each age-group. Note the change of scales for ages 5 and 6.

1 and 2, and natural mortality is the same for all sizes of fish. At later ages some minor asymmetry appears, but the main effect is that the calculated mean size at age 1 decreases gradually up to age 6 — most rapidly between ages 3 and 5, when most of the fish in the population are being subjected to differential mortality. Calculated average sizes are summarized in column 2 of Table 6.

Instead of taking a representative sample at the start of each year, a representative sample might be taken from the commercial catch, which frequently is distributed more or less evenly throughout the year. In that event the back-calculated age-1 mean lengths will be a little less, because of the selective mortality that occurs during the year; the estimates in column 3 of Table 6 were obtained by interpolation between the values in column 2.

Over the whole 5 years there is a decrease in back-calculated average 1st-year length from an even 100 mm down to 94.9 mm. The sample standard deviation in 1st-year length also remains close to its initial value of 10.10 mm; its computed value is 10.17 mm at age 7; with Sheppard's adjustment

TABLE 6. Model B: Comparison of mean computed lengths at age 1, from representative samples and from catches. The true mean size of the year-class at age 1 is an even 100 mm.

1	2	3	4	5
	Size (*mm*) at age 1, as calculated from:			
Age when sampled	Representative samples at the start of the year	Representative samples during the year	Catch taken during the year	Difference between columns 4 and 3
2	100.0			
		99.5	111.1	11.6
3	98.9			
		98.0	101.7	3.7
4	97.0			
		96.2	97.9	1.7
5	95.3			
		95.1	95.5	0.4
6	94.9			
		94.9	94.9	0.0
7	94.9			
		94.9	94.9	0.0

the population value becomes 10.07.[10] Computations of a values from expression 1 are made for this population on p. 505. We may observe here that the sum of the d-values for all 5 years of recruitment in Table 5 is 5.12 mm, and final s = 10.07 mm, hence for the 5 years:

$$a = 5.12/10.07^2 = 0.050 \text{ per mm.}$$

The increase in cumulative Z with length at age 7 is not completely regular (column 41 of App. Table 1, Appendix 2), but the difference between the smallest and the largest of the 16 length-classes is 3.6, so the average is close to 3.6/15 per 5 mm or 0.048 per mm. This agrees well with the 0.050 above.

From expression 2, the selectivity index for the whole period of recruitment is:

$$r = 1.349 \times 0.048/10.07 = 0.64$$

Thus the larger half (initially) of the year-class was subjected to an average rate of fishing greater by 0.64 than that which the smaller half experienced — this differential being spread over 5 years.

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[10] This slightly high value, as well as the slightly low value for computed mean length (94.9 instead of 95.0), and the slight asymmetry of the distribution for age 6 and on, are partly artifacts caused by the grouping interval. However, the cumulative Z that successive length-classes have been exposed to does not increase completely regularly with size (column 41 of App. Table 1, Appendix 2), and this should produce some asymmetry.

Rates of Fishing and Growth Rates from Representative Samples

The sums over individual length-classes (here represented by the subscript *i*) at each age in Model B make it possible to compute the following statistics for each age-group as a whole (data from App. Tables 1 and 2 of Appendix 2):

$$F = \frac{\Sigma(F_i \overline{N}_i)}{\Sigma \overline{N}_i} = \frac{\Sigma C_i}{\Sigma \overline{N}_i} : \text{numerical rate of fishing}$$

$$F_W = \frac{\Sigma(F_i \overline{B}_i)}{\Sigma \overline{B}_i} = \frac{\Sigma Y_i}{\Sigma \overline{B}_i} : \text{ponderal rate of fishing}$$

Adding the constant $M = M_W = 0.2$ to F and to F_W gives Z and Z_W.

The results indicates the effect of gradual recruitment on the age-group statistics of biomass change (Table 7). The numerical rate of fishing (row 5) increases gradually from $F = 0.098$ at age 2+ to $F = 1.3$ at age 6+. The ponderal rate of fishing, F_W in row 9, is larger than F at all ages until full recruitment is achieved, but the absolute difference is never very great: only 0.02–0.03.

Growth statistics are computed from the average lengths shown in Table 5, using expressions 4 and 6. The magnitudes of G and G_X in rows 15 and 16 of Table 7 differ similarly to the mortality statistics: in fact, values of $G-G_X$ in row 17 agree with F_W-F or Z_W-Z in row 12, within the accuracy of the computations, as is required by expression 11 above.

Change in Vulnerability among Larger Fish

The concept of "full recruitment," that is, a length interval over which vulnerability to the fishing in progress is substantially uniform, is almost indispensable to the analysis of population statistics. By tagging and in other ways it has been shown for some populations that such an interval or asymptote does exist (e.g. Hickling, 1938; Ricker, 1949), but more often this must be assumed. With gears that are intrinsically nonselective above a certain fish size the whole upper range of lengths in the population *may* be equally vulnerable — though changes in behaviour or distribution with size sometimes spoil the picture. When the gears in use, gillnets for example, are known to be intrinsically quite selective by size, there is still an intermediate length range within which maximum vulnerability occurs, and which will usually have a fairly broad dome of almost-uniform vulnerability on either side of the maximum. This stems mainly from the fact that fishermen will normally use the combination of meshes or hook sizes that bring them maximum poundage returns within the saleable size range; thus small young fish and (sometimes) scarce old fish tend to be taken less frequently than those of intermediate size.

In general, then, after full recruitment is achieved vulnerability may remain constant up to the maximum size present, or it may decrease among

TABLE 7. Model B: Statistics of mortality and growth for successive age-groups. Values for fish older than 7+ are extrapolated.

	Symbol	Year of life								
		1+	2+	3+	4+	5+	6+	7+	Older	Total
1. Stock at start of year	N	100000	81868	60786	29921	8472	1934	431	123	283535
2. Mean stock	$\bar{N}$	90634	70703	43411	16596	4427	1002	223	63	227419
3. Catch ($=F\bar{N}$)	C	0	6939	22180	18057	5646	1303	290	83	54498
4. Numerical mortality rate	Z	0.200	0.298	0.711	1.265	1.475	1.500	1.500	1.500	–
5. Numerical rate of fishing	F	0	0.098	0.511	1.065	1.275	1.300	1.300	1.300	–
6. Biomass at start of year	B	103.1	280.0	350.9	267.1	97.5	28.6	7.6	2.5	1137.3
7. Mean biomass	$\bar{B}$	179.1	313.4	304.1	167.8	56.2	15.9	3.9	1.3	1041.3
8. Ponderal mortality rate	Z_W	0.200	0.319	0.742	1.287	1.481	1.500	1.500	1.500	–
9. Ponderal rate of fishing	F_W	0	0.119	0.542	1.087	1.281	1.300	1.300	1.300	–
10. Yield ($=F_W\bar{B}$)	Y	0	37.3	164.8	182.5	71.9	20.6	5.1	1.6	483.8
11. $F\bar{B}$	–	0	30.7	155.4	178.7	71.6	20.6	5.1	1.6	463.8
12. $Z_W-Z=F_W-F$	–	–	0.021	0.031	0.022	0.006	0.000	0.000	–	–
13. Observed mean length	L	100.0	150.0	178.9	207.0	225.3	244.9	259.9	–	–
14. Back-calculated length	L_C	100.0	148.9	177.0	205.3	224.9	244.9	259.9	–	–
15. Rate of growth	G	1.216	0.551	0.470	0.279	0.256	0.178	0.168	–	–
16. "X" rate of growth	G_X	1.216	0.528	0.438	0.254	0.250	0.178	0.168	–	–
17. $G-G_X$	–	0	0.023	0.032	0.024	0.005	0.000	0.000	–	–

the largest fish. Exceptionally it may increase in later life, for example if the largest fish acquire "trophy" value and are specially sought after on that account. However, since large fish generally increase in length much more slowly than small ones, many ages may be represented at a given length in the upper part of the population's size range, so that any given change in rate of fishing (F) per unit of length has far less effect on observed and back-calculated mean sizes than it has during the recruitment phase. This has been confirmed by numerical models, but it is scarcely necessary to reproduce them here.

SELECTIVE MORTALITY FROM NATURAL CAUSES

Identification of "Natural" Lee's Phenomenon

Little can be said about the nature of natural selective mortality. There is some experimental evidence that faster-growing fish tend to mature earlier and also die earlier than their slower-growing siblings. This may reflect a direct physiological connection between maturity and mortality, or it may be that spawning is followed by temporary exhaustion that makes the fish more vulnerable to disease. In the wild, it is also possible that the spawning activities themselves involve dangerous behaviour and make fish more vulnerable to predators.

Where natural differential mortality exists, there is of course a ponderal natural mortality rate, M_W, that differs from the numerical rate M. Natural differential mortality can readily be detected and measured in the following situations, *if representative samples are available of each age-group*: (1) when Lee's phenomenon is discovered in unfished stocks; (2) when it occurs in portions of a stock for which rate of fishing and natural mortality rate are known to be uniform; (3) when it occurs during recruitment ages in too pronounced a form to be accounted for by the increase in rate of fishing with size.

A puzzling feature of differential mortality in unfished stocks is its sporadic occurrence. For example, the Silver Lake ciscoes of Fig. 1 have Lee's phenomenon strongly developed, the stock being an unfished one. However, among the ciscoes of three other unfished lakes of northern Wisconsin Hile (1936) found only weak and marginally demonstrable Lee's phenomenon.

Where a fishery exists, any Lee's phenomenon discovered among age-groups considered uniformly catchable (as indicated by recaptures of tagged individuals, for example) is to be ascribed to natural causes.

During recruitment ages there may be a mixture of natural and gear-caused selective mortality. An attempt can be made to separate the two provided the samples available are not biassed, which means they must *not* be from the commercial catch. Trial computations, similar to Model B here, can be made to get an idea of the amount of Lee's phenomenon that is likely to be caused by the probable change in catchability with size, as estimated from the observed lengths and the nature of the gear in use. However, Model B itself suggests that fishing has to be intensive, and that recruitment must be prolonged over several years, in order to produce even quite a moderate degree of Lee's phenomenon (Table 5).

NEGATIVE SELECTIVE MORTALITY

Selection needn't always be positive, i.e., in the direction of greater mortality among the larger fish of a particular age. The reverse is quite possible biologically, for example if predators or parasites kill more of the smaller individuals of an age-group than of the large. Negative selection may well be fairly common during the first few years of life. For one thing, any selective effects of predation or other mortality acting on a brood during age 0+, prior to the time of the first annulus, cannot be discovered by ordinary scale reading, and this is the period during which smaller fish would be likely to suffer most heavily. Furthermore, often samples of fish of one or more of the younger ages are not available, or if available they are badly biassed toward the larger individuals. Thus direct information on growth and selectivity of mortality at early ages is actually very scarce. At older ages also, bias in sampling will always act to suppress the evidence of any negative selective mortality that may exist (p. 508).

QUANTITATIVE INTERPRETATION OF LEE'S PHENOMENON WHEN SAMPLING IS UNBIASSED

COMPUTATION OF a AND r

Back-calculated lengths of fish are commonly tabulated in the manner shown by Table 5, or by the "A" entries in Tables 1 and 4. In these tables the entries of successive horizontal rows constitute the sample lines referred to earlier (p. 482). These lines are of course not wholly distinct and separate. Each sample is taken from the whole population surviving at that time, which naturally includes some of the same fish as can be taken in any of the later samples. For this reason abrupt differences in growth rate between successive lines are not to be expected; if they occur, the data should be checked for errors in calculation, inadequate sample size, or the effects of any difference in growth rate between different year-classes (when more than one is involved).

The term Lee's phenomenon is commonly applied to the whole of the length entries in Tables such as 1, 4, and 5, insofar as the lengths tend to decrease progressively down the columns. However, for quantitative purposes, the two right-hand entries of each row of these tables are the most useful ones. Only these are a direct reflection of selectivity in the mortality at each age, and only these can be used in the computations of expressions 1 and 2 above. It is not at all uncommon for the sign of the difference between calculated terminal and penultimate lengths of two adjacent sample lines to differ from that of the difference between the calculated 1st-year lengths in the same two lines (Tables 15 and 16 below).

Numerical models A and B above are special cases, but they shed light on these relationships. Model A fish (Tables 2–4) are subjected to continuing selective mortality throughout life, of the same intensity at all ages: a = 0.02 per millimetre. Applying expression 1 to the figures in Table 4 makes it possible to compute the standard deviation (s) in length at successive ages.

As an example, for age 3+:

$$s^2 = (187.0-183.1)/0.02 = 195$$
$$s = 14.0 \text{ mm}$$

The complete set of values is as follows:

Age	s	Age	s
1+	10.0	4+	15.0
2+	12.8	5+	17.7
3+	14.0		

Notice that the same difference, 3.9 mm, is obtained between all adjacent pairs of lengths within column 5 of Table 4. This consistency is present at the other ages as well, so that s for all ages could be computed from the last two rows alone.

In Model B (Table 5) all the fish of a given age increase in length by the same amount, and differential mortality changes the survivors' standard deviation in length very little, the population value being close to $s = 10$ at all ages when adjusted for grouping. The amount of selection varies as the fish get older. Consequently expression 1 can be used to compute the average amount of within-age increase in Z, per millimetre of length, for each age. The differences (d) are shown at the foot of Table 5. Using age 3+ as an example:

$$a = d/s^2 = 1.87/100 = 0.0187 \text{ per mm.}$$

This can be checked approximately by a direct computation. The Z-values at age 3+ (column 16 of App. Table 1, Appendix 2) increase by 0.1 per 5 mm between all length-classes except the two smallest. Hence mean a would be slightly less than 0.02 per millimetre, in agreement with the above. The complete set of Model-B a-values is as follows:

Age	a	Age	a
1+	0	5+	0.0042
2+	0.0114	6+	0.0002
3+	0.0187	7+	0
4+	0.0167		

In Model B the length differences are the same across the horizontal rows of Table 5, so that the selectivity at all ages can be calculated from column 2 alone.

Thus, both in Model A and in Model B calculated lengths at ages earlier than the penultimate one bear a fixed relation to successive pairs of lengths at the margin of the table. However, this relationship is not at all the same for the two models, and each derives from a particular simplifying condition used in the model's construction (constant selectivity for A, uniform increase in length for B). In nature neither of these conditions is likely to exist, and back-calculated lengths at the earlier years will be determined by a combination of selectivity and growth pattern in successive years that has not yet been analyzed into its component parts. Such an analysis may not be impossible, but it doesn't seem to be simple. It would be a useful thing to have in the frequently occurring situation where representative samples of the younger ages are not available.

At the moment, then, back-calculated lengths for earlier years can be used only qualitatively to suggest the nature of selection during the first few years of life.

VARIABILITY IN LENGTH AND GROWTH COMPENSATION

Rodney Jones's (1958) discovery — that selective mortality need not change the shape or variability of a length-frequency distribution — makes it easy to understand why in most fish populations lengths do remain reasonably symmetrical throughout life. Variability is another matter, however, for the fish are growing, and a variety of factors can affect their standard deviation in length as time goes on.

Actually, remarkably few people have taken the trouble to compute the variability in length of the fish they were studying. For a population of bluegills, Ricker (1942, p. 203) found that standard deviation at first increased with age, and later decreased somewhat. Another example is the stock of sprats shown in Table 14 below: ignoring the oldest group, represented by only six individuals, it appears that these fish are more variable in length at age 2 than at age 1, and later become somewhat less variable. The same pattern has been observed in other populations, though sometimes the increasing phase is restricted to the 1st year of life so that the fish have reached their maximum variability at age 1.

Why should the lengths of the fish in a year-class vary less as the fish become older and larger ? Growth is primarily a matter of increase in bulk, and during very early stages of life all the fish in a brood tend to increase in weight exponentially. If the exponent is the same at all sizes, this means that the absolute disparity in weight between large and small individuals tends to *increase*. Even after increase in weight is no longer exponential, it usually continues for some time to be such that variability in weight of the year-class increases. This phase may last for several years, but after a while the smaller fish usually start to catch up with the larger ones. Scott (1949) points out that during the time that variability in weight is still increasing the variability in length will start to decrease, because of the power relationship between length and weight. This decrease often begins during the 2nd year of life, and rarely later than the 3rd. Thus a moderate decrease in standard deviation in length with age is, in a sense, an "accidental" consequence of the weight–length relationship.

Considering the same phenomenon from the point of view of lengths alone, it is a matter of observation that absolute increase in length is typically less among the larger than among the smaller fish of an age-group, so that there is a tendency for the smaller ones to catch up to the larger ones (Sund, 1911, and many later authors). This is known as "growth compensation," and one of its results is the negative correlation between length increments in successive years of a fish's life that has been demonstrated in many fish stocks. Positive correlations ("growth depensation") are also known, but only between ages 1 and 2, or rarely 2 and 3 — although, in terms of *weight*, depensation is of course the rule during the first several years of life at least. Weight too may tend to become less variable among the older ages of some stocks, but this point has been little studied.

Thus growth compensation is a cause, or an aspect, of the decrease in variability in length that occurs as a year-class grows older. Does it also affect Lee's phenomenon? The question arises because Van Oosten (1929, p. 337), who observed growth compensation in the ciscoes of Lake Huron, cited it as one possible reason for the fact that among them Lee's phenomenon tended to disappear or to be reversed during later years of life. This seems plausible because if the initially smaller fish are catching up to the initially larger ones, their scale increments will certainly reflect it. But this does not mean that computed lengths at earlier years will be disproportionately changed. Numerical models show that growth compensation can neither produce nor remove Lee's phenomenon. In the absence of selective mortality back-calculated mean lengths are always the same as the actual mean lengths of the population, at all earlier ages, regardless of how growth may vary with length within age-groups.

VARIABILITY IN LENGTH AND SELECTIVE MORTALITY

Does size-selective mortality ever contribute to the change in variability in length of a year-class as it grows older? If the shape of the within-brood change in instantaneous mortality rate with length is not linear, then an effect on variability is theoretically possible. But it is not easy to imagine situations where this would be appreciable. Suppose, for example, that there is a trout fishery with a rigidly enforced minimum size limit, and an age-group with normal length distribution happens to be half vulnerable and half protected. During a brief but fairly intensive fishery ($F = 0.7$) half of the vulnerable group is removed. A calculation shows that the effect is to reduce the variability (s^2) in length of the age-group by only 8%, and the standard deviation (s) by 4%.

Another possible situation occurs where the fishery is more protracted and during its activity half of a brood *grows into* the vulnerable size range at a steady rate. In that event the decrease in variability is close to 4%, and in s is 2%, with $F = 0.7$ and no natural mortality. If all of the brood grows into the vulnerable size range while the fishery operates there is no permanent reduction in variability at all, in spite of the "knife-edge" selection.

We may conclude that any effects of selective mortality on variability in length among natural populations are almost certain to be inconsequential and unrecognizable.

BIAS IN SAMPLING

When an example of Lee's phenomenon is encountered in nature, it is necessary to decide to what extent sampling bias may contribute to it, before attempting any interpretation based on selective mortality. The possible vulnerability-size relationships of sampling gear are the same as those of commercial gear discussed on p. 501, with the exception that sampling gear may be specially selected to have a flat vulnerability spectrum, or different gears may be chosen to sample different size ranges. Often, however, the only samples available are those taken from the commercial catch, in which event sampling bias and selective mortality are intimately associated.

SAMPLING BIAS IN THE ABSENCE OF SELECTIVE MORTALITY

To examine effects of sampling bias when there is no selective mortality a simple trial population (Model C) will be used in which fish of all sizes and at all ages have the same total mortality rate: $Z = 0.75$, $S = 0.472367$. The length frequency distribution at age 1 has the same normal distribution as in column 4 of Table 2. From age 1 onward all fish of a given age increase in length by the same amount, this being 65, 25, 25, 20, 15, and 10 mm in successive years. The stock is assumed to be large enough that the samples taken do not affect its survival rate appreciably.

For each sampling regime the number and average length of the fish sampled at each age was determined. Results are set forth in tables of the usual type for Lee's phenomenon, and compared with the results of random sampling. The sampling regimes used were as follows: (1) Vulnerability increases by 0.02 per 5 mm throughout, starting at 0.02 for the smallest length-class (60–65 mm) (Table 8, A lines). (2) Vulnerability decreases by 0.02 per 5 mm throughout, starting at 1.00 for the smallest length-class (Table 8, C lines). (3) Vulnerability increases by 0.05 per 5 mm, starting at length-class 100–105 mm; it has risen to 1.00 at length-class 195–200 mm, and remains steady thereafter (Table 9, A lines). (4) Vulnerability is zero through the 75–80 mm length-class; it increases in an ogive pattern to reach 1.00 in the 175–180-mm group; it remains constant through the 220–225-mm group; and thereafter it decreases by 0.05 per 5 mm (Table 9, C lines).

The true distribution of mean length in the Model C population is given by the B lines in Tables 8 and 9. It is obvious that, when vulnerability increases with size, the average length of any age-group in a sample is greater than its true length (A lines), and the reverse is true when vulnerability decreases (C lines).

However, if either the A or the C lines in these tables were obtained by observation, no such standard of comparison would be available. The pertinent information would be limited to the differences (*d* in expressions 1 and 2 above) between the calculated length at each terminal annulus and the length at the penultimate annulus of the next older sample line, which are summarized at the foot of Tables 8 and 9. The fact that all these differences are positive

TABLE 8. Model C: Simulation of back-calculated lengths when there is sampling bias but no selective mortality. A: vulnerability to sampling gear increases with length; B: completely representative sampling; C: vulnerability to sampling gear decreases with length.

Sampling age		Back-calculated lengths at successive ages (*mm*)						
		1	2	3	4	5	6	7
	A	*102.400*						
1	B	100						
	C	**99.520**						
	A	*100.949*	*165.949*					
2	B	100	165					
	C	**99.308**	**164.308**					
	A	*100.770*	*165.770*	*190.770*				
3	B	100	165	190				
	C	**99.168**	**164.168**	**189.168**				
	A	*100.648*	*165.648*	*190.648*	*215.648*			
4	B	100	165	190	215			
	C	**98.954**	**163.954**	**188.954**	**213.954**			
	A	*100.575*	*165.575*	*190.575*	*215.575*	*235.575*		
5	B	100	165	190	215	235		
	C	**98.683**	**163.683**	**188.683**	**213.683**	**233.683**		
	A	*100.530*	*165.530*	*190.530*	*215.530*	*235.530*	*250.530*	
6	B	100	165	190	215	235	250	
	C	**98.530**	**163.530**	**188.530**	**213.530**	**233.530**	**248.530**	
	A	*100.504*	*165.504*	*190.504*	*215.504*	*235.504*	*250.504*	*260.504*
7	B	100	165	190	215	235	250	260
	C	**98.059**	**163.059**	**188.059**	**213.059**	**233.059**	**248.059**	**258.059**
	A	*1.451*	*0.179*	*0.122*	*0.073*	*0.045*	*0.026*	–
d-values	B	0	0	0	0	0	0	–
	C	**0.212**	**0.140**	**0.214**	**0.271**	**0.153**	**0.471**	–

shows that *there is positive Lee's phenomenon at all ages, whether vulnerability to the sampling gear is increasing or whether it is decreasing.*[11] This apparently paradoxical situation was noticed and illustrated some years ago (Ricker, 1942, p. 173). It stands in direct contrast to the effect of selective mortality, which produces positive Lee's phenomenon only when mortality increases with length within age-groups, and produces negative Lee's phenomenon when mortality decreases with length.

The magnitude of the sampling-bias Lee's phenomenon at any age depends on the population's *absolute* rate of increase in length (faster increase, greater LP), and on the *relative* rate of change in vulnerability to the sampling gear

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[11] This rule is not completely universal. Negative Lee's phenomenon appears when vulnerability is decreasing with length and the percentage change in vulnerability from one length-class to the next decreases: for example, a sequence of vulnerabilities such as 1, 0.819, 0.677, 0.566, 0.477, 0.407, 0.350, 0.304, 0.267, 0.237, etc. However, I have not been able to imagine natural circumstances where such a pattern of vulnerability would be plausible.

TABLE 9. Model C: Simulation of back-calculated lengths when there is sampling bias but no selective mortality. A: vulnerability to sampling gear increases up to length-class 195–200 mm, then remains steady; B: completely representative sampling; C: vulnerability to sampling gear increases up to length-class 175–180 mm, remains steady through length-class 220–225 mm, and declines thereafter.

Sampling age		Back-calculated lengths at successive ages (*mm*)						
		1	2	3	4	5	6	7
	A	*111.497*						
1	B	100						
	C	**111.782**						
	A	*101.511*	*166.511*					
2	B	100	165					
	C	**100.661**	**165.661**					
	A	*100.868*	*165.868*	*190.868*				
3	B	100	165	190				
	C	**100.026**	**165.026**	**190.026**				
	A	*100.039*	*165.039*	*190.039*	*215.039*			
4	B	100	165	190	215			
	C	**99.769**	**164.769**	**189.769**	**214.769**			
	A	*100*	*165*	*190*	*215*	*235*		
5	B	100	165	190	215	235		
	C	**98.948**	**163.948**	**188.948**	**213.948**	**233.948**		
	A	*100*	*165*	*190*	*215*	*235*	*250*	
6	B	100	165	190	215	235	250	
	C	**98.596**	**163.596**	**188.596**	**213.596**	**233.596**	**248.596**	
	A	*100*	*165*	*190*	*215*	*235*	*250*	*260*
7	B	100	165	190	215	235	250	260
	C	**98.369**	**163.369**	**188.369**	**213.369**	**233.369**	**248.369**	**258.369**
	A	*9.986*	*0.643*	*0.829*	*0.039*	*0*	*0*	–
d-values	B	0	0	0	0	0	0	–
	C	**11.121**	**0.635**	**0.257**	**0.821**	**0.352**	**0.227**	–

(faster change, greater LP). The combination of these two unrelated influences makes the *d*-values in Tables 8–9 vary irregularly with age in some instances.

Because only positive Lee's phenomenon can arise from biassed sampling, it follows that *if significant negative Lee's phenomenon is actually observed, it is certain to have been caused by selective mortality of one sort or another*. Of course the *magnitude* of an observed negative LP does not necessarily correspond to the degree of negative selection that prevails in the population. What is observed may be only a minimum value, for biassed sampling can have reduced its full effect on the back-calculated lengths.

SAMPLING BIAS COMBINED WITH SELECTIVE MORTALITY

The model used to examine this situation (Model D) has the selective mortality of Model A and the growth pattern of Model C (the same absolute length increment for all fish of a given age). This is combined with the continuous increase in vulnerability of sampling regime 1 on page 508 (A lines of Table 10); and also with the continuous decrease in vulnerability of sampling regime 2 (C lines of Table 10). The B lines of the Table are the mean lengths that would be obtained from perfectly representative sampling, as calculated from the means in Table 2.

As before, when vulnerability to the sampling gear increases with size, it makes the lengths computed from the sample greater than the population values; and vice versa. Both the increasing and the decreasing sampling regimes increase the magnitude of the Lee's phenomenon that appears in the back-calculated lengths (lines A and C at the foot of Table 10) — that is, the paradox mentioned on page 508 appears in this situation also.

TABLE 10. Model D: Simulation of back-calculated lengths when there is sampling bias and positive selective mortality. A: vulnerability to sampling gear increases with length; B: completely representative sampling; C: vulnerability to sampling decreases with length.

Sampling age		Back-calculated lengths at successive ages (*mm*)						
		1	2	3	4	5	6	7
	A	*102.657*						
1	B	100.000						
	C	**99.520**						
	A	*98.927*	*163.927*					
2	B	97.960	162.960					
	C	**97.278**	**162.278**					
	A	*96.714*	*161.714*	*186.714*				
3	B	95.921	160.921	185.921				
	C	**95.118**	**160.118**	**185.118**				
	A	*94.558*	*159.558*	*184.558*	*209.558*			
4	B	93.886	158.886	183.886	208.886			
	C	**92.906**	**157.906**	**182.906**	**207.906**			
	A	*92.453*	*157.453*	*182.453*	*207.453*	*227.453*		
5	B	91.856	156.856	181.856	206.856	226.856		
	C	**90.674**	**155.674**	**180.674**	**205.674**	**225.674**		
	A	*90.389*	*155.389*	*180.389*	*205.389*	*225.389*	*240.389*	
6	B	89.837	154.837	179.837	204.837	224.837	239.837	
	C	**88.454**	**153.454**	**178.454**	**203.454**	**223.454**	**238.454**	
	A	*88.358*	*153.358*	*178.358*	*203.358*	*223.358*	*238.358*	*248.358*
7	B	87.836	152.836	177.836	202.836	222.836	237.836	247.836
	C	**86.296**	**151.296**	**176.296**	**201.296**	**221.296**	**236.296**	**246.296**
	A	*3.730*	*2.213*	*2.156*	*2.105*	*2.064*	*2.031*	–
d-values	B	2.040	2.039	2.035	2.030	2.019	2.001	–
	C	**2.242**	**2.160**	**2.212**	**2.232**	**2.220**	**2.158**	–

POPULATION STATISTICS FROM SAMPLES OF THE COMMERCIAL CATCH

A situation of special importance occurs where catch samples from a large-scale fishery are used to estimate growth rates and mortality rates. A majority of fishing gears "favour" the larger members of the younger age-groups. This is especially true of commercial fishing, where small fish usually are not wanted. Hart (1948), among others, has discussed this, and has shown its quantitative effect on estimates of mean size of butter soles surviving at each age. In this case size selection was associated with earlier maturity of faster-growing individuals: these became vulnerable to fishing when they joined the spawning schools in shallow water, hence were the first to become represented in catch samples. Many herring fisheries, too, are based on spawning or prespawning assemblages, and scale samples taken from them have been discussed at length by Lea (1913) and Runnström (1936).

Sampling bias is most serious in estimating mortality rate, for it is necessary that adjacent age-groups be equally vulnerable in order to compare their abundance directly. For growth studies it is "only" required that all fish of each particular age be equally vulnerable to one type of year. But in practice this makes little difference when the only data available are samples from the commercial catch; the problem is to extract the most reliable information possible from such data.

GROWTH RATES FROM CATCH SAMPLES

Model B above can be used to examine the usefulness of catch samples in the situation where fishing effort and the growth of the fish vary in similar fashion throughout the year (for other relative timing, adjustments can be introduced). We know the relative number of fish taken at each age, and their size distribution and calculated growth histories. Back-calculation of lengths (Table 11) reveals a Lee's phenomenon that must be a combination of two elements: (*a*) that due to selective mortality during recruitment, and (*b*) that due to the sampling bias that is inherent in using catch samples. Computed age-1 length frequencies from the catch samples are shown in Fig. 5, and compared with the size of the same age-groups at the *start* of each year. Also, in columns 3 and 4 of Table 6 the computed lengths at age 1 of catch samples and representative samples are compared, both being taken during

TABLE 11. Model B: Sizes of fish at age 1, as back-calculated from catch samples.

Age when sampled	Size at successive annuli (*mm*)						
	1	2	3	4	5	6	7
2+	111:08	161.08					
3+	101.72	151.72	181.72				
4+	97.90	147.90	177.90	207.90			
5+	95.49	145.49	175.39	205.49	225.49		
6+	94.86	144.86	174.86	204.86	224.86	244.86	
7+	94.86	144.86	174.86	204.86	224.86	244.86	259.86
d	–	9.36	3.82	2.41	0.63	0.00	–

the fishing season. The difference between these (column 5) represents the shift in computed mean size that would be caused by selective sampling alone.

Obviously the selective-mortality Lee's phenomenon tends to shift the computed length at age 1 to sizes progressively smaller than the true length at age 1. By contrast, the sampling-bias LP initially gives computed sizes much greater than the true age-1 size, these decreasing rapidly and eventually coinciding with the selective-mortality type at the age when the stock becomes fully recruited.

Table 12 shows growth rates calculated from the computed lengths of Table 11. Values analogous to both G and G_X, the true and the "X" growth rates, can be calculated in the same way as in Table 7; they will be distinguished by the subscript "U." It turns out that the estimates of G_U are very close to true G except in the youngest age-group (line 7). The reason they tend to be slightly less than G is because when all the fish of an age-group increase in length by the same quantity, the larger ones have a somewhat slower instantaneous rate of increase in weight. If our model were more realistic and allowed for increase in variability in length during the 1st year or two, then the difference between G and G_U at those ages would be somewhat greater than shown here. Beyond age 3 standard deviation does not usually increase much more, and in old age it tends to decrease, as noted earlier. On the whole then, the pattern observed in the model should apply fairly well to many natural stocks, but often with a somewhat greater $G–G_U$ difference at the youngest ages.

Considering now the G_{UX} growth rates, they obviously deviate much more from G (Table 12, line 8) than do the G_X values based on representative samples (Table 7, line 17). That is, they rather seriously underestimate the true growth rate, especially at the youngest ages. If back-calculation is not possible, then the UX type of growth rates will be the only ones available from catch samples, and some kind of adjustment for them during recruitment ages becomes essential.

In general, biologists should find it easy to recognize any situation where size-at-age growth estimates deviate seriously from true growth rates. Given only the catches and G_{UX} values of Model B, two things at once suggest that G_{UX} for age 2+ must be much smaller than true G: the fact that fewer fish were captured at age 2+ than at age 3+; and the fact that G_{UX} for age 2+ is smaller than for age 3+, which would be an unusual growth pattern for fish of these ages. Thus we would automatically discount the figure 0.361 in line 4 of Table 12, and replace it by something considerably larger than 0.404, perhaps guessing at 0.5 or 0.6 as the true G. At ages 3+ and older the deviation of G_{UX} from true G would be less easy to estimate. However it would be evident that at least the age 3+ value is too small, and any informed guess at an adjustment would be better than using a value known to be biassed.

Another feature of "UX" growth rates from catch samples is that they normally apply to a different calendar interval than those obtained by back-calculation. The actual interval depends partly on the distribution of fishing

TABLE 12. Model B: Unadjusted growth rates (G_U and G_{UX}) computed by back-calculation of catch samples to the terminal and next-to-last annuli, and a comparison with true growth rates (G).

		Growth year						
	Symbol	1+	2+	3+	4+	5+	6+	7+
1. Mean length at terminal annulus (at start of growth year shown)	L_U	–	161.1	181.7	207.9	225.5	244.9	259.9
2. Mean length at penultimate annulus (at start of growth year shown)	L_{UC}	111.1	151.7	177.9	205.5	224.9	244.9	–
3. Catch-sample growth rate	G_U	1.115	0.541	0.468	0.279	0.256	0.178	–
4. Catch-sample "X" growth rate	G_{UX}	–	0.361	0.404	0.244	0.247	0.178	–
5. $G_U - G_{UX}$	–	–	0.180	0.064	0.035	0.009	0.000	–
6. True growth rate (from Table 7)	G	1.216	0.551	0.470	0.279	0.256	0.178	0.168
7. $G - G_U$	–	0.101	0.010	0.002	0.000	0.000	0.000	–
8. $G - G_{UX}$	–	–	0.189	0.066	0.035	0.008	0.000	–
9. $G - G_X$ (from Table 7)		0	0.023	0.032	0.024	0.005	0.000	0.000

during the year. It is also influenced by the fact that the fish of any given age that are growing into the vulnerable size range will tend to be more numerous toward the end of the year as more and more of their siblings become vulnerable. This will be evident in the catch samples, and an appropriate adjustment should be made. For Model B no adjustment is necessary because of the assumption (p. 496) that mortality each year is governed by the size of the fish at the start of the year.

Mortality Rates from Catch Samples

If the only direct information on mortality rates in a population is that provided by catch figures, then no unique estimates can be made of mortality during recruitment years. However conditional estimates can be made provided (1) there are at least two ages which have the same rate of fishing and the same total mortality rate; (2) some reasonably informed estimate can be made of the natural mortality rate at all ages — such as might come, for example, from a knowledge of the age composition of the stock during an early, little-exploited, period of its history; and (3) the samples used are taken randomly from the commercial catch of all ages (including discards at sea if such fish die from the effects of handling). The method is described by Ricker (1948, p. 90; 1958, p. 143), and an example is given in Table 18 below.

The estimate or estimates of M used in such a computation do not have to be extremely precise in order to provide usable values of F and Z. For example, Table 13 compares the estimates of F and Z made from the Model B catches (Table 7) using the correct value M = 0.2, with those obtained using M = 0.15 and M = 0.25. With the last two, neither F nor Z differs from its true value to any major degree at any age.

One thing to remember is that an overall average of "apparent" mortality rates (Z′) for a population can seriously underestimate the true mean rate in the situation where recruitment is still in progress. Computing S′ from the

Table 13. Model B: Conditional estimates of rate of fishing F and total mortality rate Z for the recruitment years, using the method of Ricker (1948). The basic data are the catches and the full-recruitment mortality rate Z = 1.5, which would be estimated from the ratio of catches at ages 6 and 7. Three alternative values of natural mortality rate M are examined, of which M = 0.2 is the correct one.

1	2	3	4	5	6	7	8
		M = 0.15		M = 0.2		M = 0.25	
Age	Catch	F	Z	F	Z	F	Z
2+	6939	0.11	0.26	0.10	0.30	0.09	0.34
3+	22180	0.54	0.69	0.51	0.71	0.48	0.73
4+	18057	1.11	1.26	1.06	1.26	1.01	1.26
5+	5646	1.33	1.48	1.28	1.48	1.23	1.48
6+	1303	1.35	1.50	1.30	1.50	1.25	1.50
7+	291	1.35	1.50	1.30	1.50	1.26	1.50

catches in line 3 of Table 7 using Heincke's formula (expression 11 of Chapman and Robson, 1960), and then taking natural logarithms, gives the apparent instantaneous mortality rates (Z′) shown below. They are compared with true mean Z, found by weighting the Z values in column 6 of Table 13 by the average populations of row 2 of Table 7:

Ages included	Mean Z′	Mean Z
3 and up	0.63	0.92
4 " "	1.24	1.32
5 " "	1.47	1.48
6 " "	1.50	1.50
7 " "	1.50	1.50

EXAMPLES OF SELECTIVE MORTALITY AND SAMPLING BIAS

LANGESUND SPRATS (*CLUPEA SPRATTUS*)

Table 14 shows the back-calculated lengths ("snout to the midpoint of a line between the tips of the tail when spread naturally") of sprats sampled from the fishery at Langesund on the Skagerrak (Sund, 1911). Four comparisons between final and penultimate back-calculated lengths can be made; the two younger ones indicate positive Lee's phenomenon, whereas the two older ones are negative. Sund used the direct-proportion method of back-calculation, and this might have contributed some "artificial" Lee's phenomenon at the younger ages, but its effect at older ages would be negligible. The main part of the positive LP at younger ages is, however, undoubtedly a combined effect of selective mortality and sampling bias, both caused by the poor representation of smaller sprats on the fishing grounds.

The negative Lee's phenomenon at the older ages would reflect a real feature of the population, if random error of that magnitude could be discounted. Standard deviations are available, so the magnitude of this selection can be estimated from expression 2 as $r = -0.19$ at age 4+ and $r = -0.22$ at age 5+. The true values may be even less (numerically greater), because *bias* in sampling, in either direction, would tend to bring them closer to zero. However, the *random* sampling error of the observed lengths is large enough that we cannot be sure that these negative values are real, so it is not profitable to speculate on the cause.

SAGINAW BAY PERCH (*PERCA FLAVESCENS*)

Table 15 gives another example of negative Lee's phenomenon at older ages, for female perch in a bay of Lake Huron. El Zarka (1959, p. 389 and table 16) describes the sampling bias in these data. It results in ages 2–4, and to a slight extent 5, being represented by individuals whose mean size is larger than the age-group average. Allowing for this, the standard deviation on length of age-groups 3 and larger appears to be close to 1.0 inch, and it is possibly 0.7

TABLE 14. Back-calculated lengths and standard deviations in length (*s*, in italics) of a sample of sprats (*Clupea sprattus*) from Langesund, taken June 9, 1908. Data from Sund (1911, p. 382 and table 2e), with two corrections in the means.

Year class	Age	No. of specimens	Size when caught	Back-calculated lengths					
				1	2	3	4	5	6
1906	2+	45	13.31	7.33	12.35				
			0.822	*0.814*	*1.078*				
1905	3+	74	13.64	6.59	11.08	13.12			
			0.738	*1.002*	*1.119*	*0.828*			
1904	4+	59	14.19	6.28	10.34	12.69	13.79[a]		
			0.890	*0.815*	*1.283*	*1.189*	*0.919*		
1903	5+	28	14.98	5.86	10.29	12.79	13.92[b]	14.65	
			0.887	*1.124*	*1.387*	*1.056*	*0.950*	*0.868*	
1902	6+	6	15.58	5.41	10.19	12.92	13.89	14.79	15.32
			0.970	*0.870*	*0.682*	*0.773*	*0.812*	*0.842*	*0.891*
d	–	–	–	–	*1.27*	*0.43*	*−0.13*	*−0.14*	–

[a] Sund has 14.05.
[b] Sund has 14.02.

TABLE 15. Back-calculated lengths (total length in inches) of female yellow perch from Saginaw Bay. Data from El Zarka (1959, table 27).

Age at sampling	Sample size	Back-calculated length at successive annuli								
		1	2	3	4	5	6	7	8	9
2	15	2.9	5.0							
3	281	2.7	4.5	6.6						
4	660	2.7	4.3	5.8	7.5					
5	300	2.6	4.1	5.6	7.0	8.3				
6	39	2.7	4.1	5.5	7.3	8.6	10.0			
7	6	2.9	4.7	6.6	8.2	9.8	10.8	11.8		
8	3	3.2	5.3	7.7	9.6	10.8	12.4	13.3	13.9	
9	1	2.5	4.8	8.1	10.5	12.4	13.2	13.7	14.1	14.5
d	–	–	0.5	0.8	0.5	–0.3	–0.8	–1.5	–0.2	–

inch for age 2; this permits computation of selection indices (*r*) from expression 2, as follows:

Age	*d*	*r*	Age	*d*	*r*
2+	+0.5	+1.0	6+	−0.8	−1.1
3+	+0.8	+1.1	7+	−1.5	−2.0
4+	+0.5	+0.9	8+	−0.2	−0.2
5+	−0.3	−0.4			

The positive selection indices for age 2+, and probably age 3+, are mainly an artificat of sampling bias, but at age 4+ true differential mortality from the effect of the recruitment process may be equally important (compare Table 6). From age 5+ onward negative selection indices prevail, indicating that there is greater mortality among the smaller fish of these age-groups. This effect may be associated with the habit, among older perch, of some individuals rather abruptly switching to larger foods and increasing their growth rate. This could at the same time reduce their natural mortality rate, so that the surviving fish at older ages would more and more be those that had taken this step. Alternatively, the larger fish might tend to remain in deeper water where they were less vulnerable to the fishing in progress.

Male perch of this population grew more slowly and did not survive to as great an age as the females. However, during age 6+, the last age sampled (El Zarka's (1959) table 26), their selection index had decreased to zero after being positive at earlier ages.

TIPPECANOE RIVER ROCK BASS (*AMBLOPLITES RUPESTRIS*)

The stock of rock bass studied by Scott (1949) has a rather unusual pattern of calculated growths (Table 16). This stock was fished only very lightly, so the growth relations shown result almost wholly from natural causes; and Scott concluded that fish of age 3 and older were sampled randomly by the gear he used.

TABLE 16. Back-calculated growth (fork length in millimetres) of Tippecanoe River rock bass of the 1940 year-class sampled in three successive years. From table 17 of Scott (1949).

Age when captured	Sample size	Back-calculated size at successive annuli				
		1	2	3	4	5
3+	198	41.6	87.8	135.3		
4+	162	41.9	86.3	130.6	175.3	
5+	38	42.4	82.9	121.0	157.8	188.7
d	–	–	–	4.7	17.5	–

The computed sizes of these rock bass at the last and next-to-last annuli have the normal positive pattern of Lee's phenomenon, and it is quite strongly developed. Using 13 mm as the approximate standard deviation in length at ages 3 and 4 (from Scott's tables 11–13), the selectivity index is $r = 0.49$ for age 3+ and as much as 1.8 for age 4+. In spite of this, age-1 lengths computed from older ages are slightly *greater* than those computed from younger ages. Although no quantitative interpretation of this fact can be made, it suggests that there must be negative selection among the fish of age-group 1+, and possibly 2+ as well.

EXAMPLE USING CATCH SAMPLES TO COMPUTE POPULATION STATISTICS

The haddock (*Melanogrammus aeglefinus*) on Georges Bank are one of the most intensively investigated commercial fish stocks in North America. We will not here attempt any review of all the available data concerning this stock, but rather use it to illustrate what might be done when the only age samples available are from the commercial catches.

During the 1930's and 1940's fishing effort on haddock was fairly stable and without any long-term trend. The data used below are mainly from two papers by Taylor (1958a, b). Unfortunately Taylor's data series are usually not complete for all ages, but it is possible to supplement them with information from a paper by Graham (1952).

Taylor (1958a) gives the computed fork lengths of haddock from Subareas J and M of Georges Bank over the years 1931–47. In spite of the large number of fish involved (1910 for J, 3015 for M) the data are not completely free of irregularities; we will use the unweighted average of the two (Table 17 here), which is more consistent than either one individually. The terminal values were extrapolated using the Walford line of Fig. 6 below, giving 61.1 mm for age 7, 63.5 for 8, and 65.5 for 9.

The growth curve used by Graham is shown in Table 17 for comparison. Agreement is reasonably good with Taylor's last-annulus sizes from age 3 onward, and we will, with some hesitation, treat Graham's age 2 figure also as being a reflection of the size of the fish in the catch. However, it is clear that at age 1 Graham was influenced mainly by back-calculated values, so an estimate of G is available for age 1+, though we lack any factual estimate of $G–G_X$ for this age.

TABLE 17. Back-calculated fork lengths (cm) of haddock from Subareas J and M of Georges Bank 1931–47, from Taylor (1958a), and a comparison with lengths taken from the growth curve of Graham (1952, fig. 5). See text for growth at older ages.

Age at capture	Age at annulus	Length at successive annuli 1	2	3	4	5	6	No. of fish sampled
3+	3	19.65	34.00	44.20				2014
4+	4	18.75	32.50	42.55	49.85			1768
5+	5	18.25	31.45	31.40	48.90	54.45		822
6+	6	17.95	30.90	40.55	48.20	53.85	58.10	321
		Lengths from Graham's growth curve						
		19.5	34.7	44.6	50.4	54.4	57.8	

Instantaneous rates of growth in weight will be taken as three times the difference of natural logarithms of length. Kohler (1960) determined a weight–length exponent of 2.98 for gutted haddock, which suggests the whole-weight figure must be close to 3.

Survival and total mortality rates for these fish over much the same period of years as the growth data cover can be estimated from table 1 of Taylor (1958b), which shows catch per day at successive ages. Summing the 15 complete year-classes gives the figures in column 2 of Table 18 from age 3+ through 8+; figures for ages 1+, 2+, and 9+ are added from Graham's (1952) figure 6, scaling them to the adjacent entries in Taylor's table. The difference between the natural logarithms of these successive figures is the "apparent" value of

TABLE 18. Computation of rate of fishing and total mortality rate for successive ages of Georges Bank haddock. See the text for details.

1 Age	2 C	3 Z'	4 Z' interpolated	5 M	6 Z	7 N	8 $\overline{N}$	9 F
1+	1,830			0.2	0.213		145,420	0.013
		−2.561				130,420		
2+	23,700		−1.314	0.2	0.423		106,440	0.223
		−0.066				85,497		
3+	25,319		+0.228	0.2	0.592		64,525	0.392
		+0.522				47,306		
4+	15,021		+0.540	0.2	0.627		35,144	0.427
		+0.558				25,265		
5+	8,598		+0.585	0.2	0.666		18,446	0.466
		+0.613				12,981		
6+	4,656		+0.699	0.2	0.699		9,331	0.499
		+0.785				–		
7+	2,123		+0.860	0.361	0.860		–	0.499
		+0.936				–		
8+	833		+0.887	0.388	0.887		–	0.499
		+0.839				–		
9+	360							

instantaneous mortality rate, Z′, in column 3, and in column 4 these are interpolated to give values for the duration of the biological year (annulus to annulus). These figures would be estimates of true Z *if* vulnerability were the same at all ages: but the latter is unlikely at younger ages, and of course the negative entries near the top of the table are nonsensical from this point of view. Values of Z′ increase with age up to age 8. This might be a result of a continuous increase in catchability with age, but in a trawl fishery this seems unlikely; the alternative is that it must reflect an increase in natural mortality rate at the older ages.

The sampling variability of the estimates for the older fish is fairly large, so it is difficult to decide when it is best to consider rate of fishing as stabilized. Lee's phenomenon can help in making a decision. Approximate values for the standard deviation (*s*) in length of haddock at each age can be estimated from table 4 of Taylor (1958a), making some adjustment for the omission of extremes of 1st-year size from that table. These are combined with differences (*d*) between terminal vertical pairs in Table 17 to compute selection indices (*r*) using expression 2:

Age	*d*	*s*	*r*
3+	1.65	3.3	0.68
4+	0.95	2.8	0.46
5+	0.60	2.0	0.41

The last two *r* values are not too different. This may suggest that $r = 0.41$ is close to the level of "natural" selective mortality, and that the larger values for the younger ages include elements of sampling bias and the effect of recruitment — particularly the 0.68 for age 3+. Such an argument is consistent with the approximate stabilization of Z′ beyond age 7. It leads to the conclusion that the Z′ values for age 6+ and older are likely to be good estimates of the true numerical mortality rates, with the corollary that natural mortality rate must increase beyond age 6.

Accepting 0.699 as an unbiassed estimate of Z for age 6+, Z can be estimated for younger ages if values for their natural mortality (M) can be postulated. Taylor (1958b) tried to evaluate M at successive ages from the regression of Z upon fishing effort, but the range of efforts available was limited and the year-to-year variation was so great that the estimates obtained were practically useless. He finally selected 0.2 as a reasonable average value for all ages, apparently mainly because figures of about this size have been discovered in other groundfish stocks. On similar grounds Graham (1952) used an annual natural mortality rate of 0.15, which corresponds to $M = 0.20$ given his total annual mortality rate of $A = 0.45$ ($Z = 0.60$).

Having no better information, we too will use $M = 0.2$ for haddock of age 6+ and younger. Columns 6–9 of Table 18 illustrate the computation of F and Z for ages less than 6+, using the method referred to on p. 515 above. The 4656 fish caught during age 6+, divided by $F_6 = 0.499$, represent a mean stock of 9331. Putting $A = 1\text{–}S$ and $S = e^{-Z}$, these correspond to an initial stock of $9331Z_6/A_6 = 12981$ at age 6. This initial stock, in turn, results from the action of an unknown rate of fishing (F_5) upon the average stock ($\bar{N}_5$) present during age 5+. Using trial values of F_5, combined with $M = 0.2$ to give a trial Z_5, $\bar{N}_5$ is estimated as $12981A_5/Z_5S_5$.[12] This, multiplied by F_5, is the catch at age 5+; and repeated trials reveal that $F_5 = 0.466$ is the 3-digit figure needed to bring $12981F_5A_5/Z_5S_5$ closest to 8598. Repetition of the same process gives values for Z and F at progressively younger ages, shown in columns 6 and 9.

On the interpretation of the data used here, column 9 of Table 18 shows that catchability increases from age 1+ through age 5+, though at 5+ it is close to the definitive value. This means that the samples taken at these ages are biassed toward the larger members of their age-groups; thus they should exibit a combination of the sampling-artifact type of Lee's phenomenon and the differential-mortality type caused by the increase in F with age (cf. p. 512). The G_U and G_{UX} growth rates of Table 19, computed from the lengths in Table 17, are therefore smaller than the corresponding rates G and G_U that would be estimated from representative samples. *However*, row 7 of Table 12 shows that G_U is quite close to G except at the youngest age; so we will be close to reality if we accept G_U as an estimate of true growth rate at ages 3+ through 5+, and if we increase it by 0.01 at age 2+ and by 0.1 at age 1+. These small adjustments are justified by the general similarity of the haddock stock to that of Model B.

For ages 6+ to 8+, where back-calculated lengths are lacking, G is estimated as being 0.02 greater than G_{UX} on the basis that growth curves that show Lee's phenomenon usually continue to do so right through to the oldest ages (cf. Fig. 1). Since we postulate no increase in catchability at these ages, the extra 0.02 must be a component of the ponderal natural mortality rate, this being greater than the numerical rate because of a more rapid die-off of larger individuals.

There remains the problem of an estimate of $G-G_X$ for the younger ages, which is needed in order to estimate ponderal rate of fishing. We cannot use G_U-G_{UX} for this estimate, because the sampling-artifact component in the catch samples makes this difference considerably greater than $G-G_X$ (cf. Table 12). Nor is there any constant ratio between the two differences. If we regard natural selective mortality as negligible at these ages, the best way to resolve the difficulty would be to construct a model similar to Model B but arranging it so that the values of G, F, Z, and duration of recruitment were of the same general magnitude as found for the haddock. Without going to this trouble, we may notice that the definitive Z is smaller for haddock than in Model B (about 0.8 as compared with 1.5), but the recruitment process lasts about a year longer. These two differences are partly compensatory, so on balance the values of $G-G_X$ in the last line of Table 12 should be applicable to haddock if they are stretched out over one more year, reduced a little in magnitude, and lined up at comparable ages. Equating age 1+ of haddock to age 2+ of the model, $G-G_X$ estimates of 0.02, 0.03, 0.02, 0.008, and 0.003 are pro-

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[12] Values of A/Z (= *a/i*) and A/ZS (= *a/is*) are tabulated in Appendix II of Ricker (1958).

TABLE 19. Computation of ponderal mortality rates (F_W and Z_W), mean biomass ($\overline{B}$), yield (Y), and production (P) for Georges Bank haddock. See text for details.

	Symbol	Year of life									
		1+	2+	3+	4+	5+	6+	7+	8+	Older	Total
1. Catch-sample growth rate	G_U	1.729	0.787	0.475	0.322	0.228	–	–	–	–	–
2. Catch-sample "X" growth rate	G_{UX}	–	0.753	0.361	0.265	0.195	0.151	0.116	0.093	–	–
3. Rate of growth	G	1.829	0.797	0.475	0.322	0.228	0.171	0.136	0.113	–	–
4. Natural mortality rate	M	0.2	0.2	0.2	0.2	0.2	0.2	0.361	0.388	–	–
5. Ponderal natural mortality rate	M_W	0.2	0.2	0.2	0.2	0.2	0.22	0.381	0.408	–	–
6. Rate of fishing	F	0.013	0.223	0.392	0.427	0.466	0.499	0.499	0.499	–	–
7. Ponderal rate of fishing	F_W	0.033	0.253	0.412	0.435	0.469	0.499	0.499	0.499	–	–
8. Numerical mortality rate	Z	0.213	0.423	0.592	0.627	0.666	0.699	0.866	0.892	–	–
9. Ponderal mortality rate	Z_W	0.233	0.453	0.612	0.635	0.669	0.719	0.880	0.907	–	–
10. $G-Z_W$	H	+1.596	+0.344	–0.137	–0.313	–0.441	–0.548	–0.744	–0.794	–	–
11. Survival rate of biomass	e^H	4.933	1.410	0.872	0.731	0.644	0.578	0.475	0.452	–	–
12. Biomass at start of year	B	203	1000	1410	1230	899	579	335	159	–	–
13. $(e^H-1)/H$	–	2.474	1.193	0.935	0.859	0.809	0.770	0.705	0.690	–	–
14. Mean biomass	$\overline{B}$	502	1193	1320	1057	727	446	236	110	–	–
15. Yield $=F_W\overline{B}$	Y	17	302	544	460	341	223	118	55	50	2110
16. $F\overline{B}$	–	7	266	517	451	338	223	118	55	50	2025
17. Production $=G\overline{B}$	P	918	951	627	340	166	76	32	12	8	3130
18. $G_{UX}\overline{B}$	–	(850)[a]	898	477	280	142	67	27	10	6	2757

[a]Estimated.

posed for ages 1+ through 5+ of the haddock stock. These figures are added to F to give the F_W values of row 7 of Table 19.

The remainder of Table 19 follows the plan of Table 7. Z_W in line 9 is the sum of lines 5 and 7. H in line 10 is the difference between 3 and 9. The initial-biomass values in line 12 start with the arbitrary figure 203 at age 1+, and are multiplied by the e^H factor immediately above to give next year's biomass to the right. The average stock factor in line 13 is multiplied by the initial stock above it to give the mean biomass in line 14. Yield is estimated as $F_W\bar{B}$ (line 15), and production as $G\bar{B}$ (line 17).

Repetition of the above calculations with different values of F at the earlier ages, or at all ages, will show what changes in the total yield and in its size composition can be expected under changed conditions of exploitation (but with constant year-class size at age 1). A computer is useful for extensive trials, using Paulik and Bayliff's (1967) program.

Graham (1952, fig. 7) performed comparable calculations, using the Beverton–Holt method apparently. His growth data (though not his treatment of them) were almost identical with those used here, but he postulated an average mortality rate of $Z = 0.60$ during the base period for all fish of ages 3+ and older. For $M = 0.2$, an increase of 30% in equilibrium yield was predicted to follow from introducing a larger mesh — 4.5 inches — in the trawls (Taylor et al., 1959, p. 19).

Increasing the mesh size means reducing the rate of fishing at the younger ages. For example, if F and F_W are reduced to 0 at ages 1+ and 2+, the immediate effect is to reduce yield by 319 units, to 1791 (Table 19). As a result, however, H becomes 1.629 at age 1+ and 0.597 at age 2+, so that after 2 years the initial stock at age 3 will be 1894 instead of 1410. After as many years as are shown in the table, the yield of ages 3+ and up increases to 1894/1410 times 1791, or 2406. The net change in yield is therefore from 2110 to 2406, an increase of 14%. If age 3+, as well, is not fished, the equilibrium yield is 20% greater than 2110; but removing additional ages starts a decline in yield. Combinations of F_W values that would simulate the selective action of a 4.5-inch trawl mesh can also be used, and the estimated increase in equilibrium yield appears to lie between the 14 and 20% above.

The 4.5-inch mesh was introduced in the early 1950's. The most recent evaluation of its effect (Graham, 1960) suggests that there was a 20% increase in weight of fish landed per unit number of age-1 fish. This check was obtained by comparing the yields of the 1948 and 1952 year-classes, from which similar *numbers* of fish were landed under the two different fishing regimes.[13]

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[13] This of course carries the implication that the rate of fishing on fully vulnerable fish remained approximately the same for the two year-classes. Even so, it is not a completely appropriate comparison, for the 1948 year-class would have experienced fewer natural deaths than the 1952 in its early years (even though its instantaneous rate of natural mortality was the same) because of the "competition" between fishing and natural mortality. Thus the 1948 year-class must have been less numerous than the 1952 at age 1, making the increase in yield due to mesh regulation somewhat less than 20%. There were of course other benefits from the big mesh, such as larger average size of fish landed, and less sorting on the vessels.

However, no comprehensive comparison of different methods of analysis can be attempted here. Each fish stock has its own individual characteristics, so that the magnitude or even the sign of the difference between two types of analysis may vary from one to another. As far as the haddock are concerned, the larger mortality rates used in Table 19, as compared with Graham's average figure of $Z = 0.6$, are mainly responsible for its providing a smaller estimate of improvement in yield. Our use of true rather than "X" growth rates at the younger ages would tend to increase, not decrease, the expectation of benefit from a larger mesh size, though quantitatively the effect is quite small.

COMPUTATIONS OF PRODUCTION AND YIELD

PRODUCTION

The term production, as defined by Ivlev, is the total elaboration of biomass by a stock of animals. It is equal to the instantaneous rate of growth multiplied by the average biomass[14] present (Ricker, 1946, 1968).

Table 20 shows this computation for the Model A population. The growth rates in rows 1–3 are from Table 4, extended one year. Values of Z are from Table 3, and Z_W is found by adding rows 3 and 4, according to expression 11. The difference between rows 1 and 5 (or 2 and 4) gives H in row 6, and $(e^H-1)/H$ in row 8 is obtained from column 5 (for age 1+) and column 4 (for the remaining ages) of Appendix II of Ricker (1958), equating H to *i* of that table. The initial biomass at each age is the product of the number of fish present (column 2 of Table 3) and their average individual weight (right-hand entry in each B line of Table 4). The mean biomass for the year, B, is the product of rows 7 and 8. The production ($G\bar{B}$) of the Model A stock, shown in row 10, adds up to 410 kg. If the G_X growth rates be used, this figure becomes reduced to 370, or by 10%.

Table 21 is a similar computation for the Model B stock. The production is 597 kg through age 6+; if the G_X growth rates be used it is 4% less.

Table 22 treats the cisco population of Table 1 in the same way, postulating a numerical mortality rate of $Z = 0.7$ throughout. The total production is 298 kg per year per 10,000 fish of age 1. Here the error that would be introduced by using the G_X growth rates is as much as 32%.

Production was also computed for the Tippecanoe rock bass population of Table 16. Estimates of mortality calculated from Scott's table 15 and text were used: $Z = 0.39$ at age 3, 0.90 at age 4, and 1.83 at age 5. These were interpolated between years and combined with the appropriate growth rates

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[14] Average biomass in this paper has been estimated from the area under the exponential curve of biomass change, that is, as $(e^H-1)/H$ times the initial biomass. Ricker (1958, p. 209) points out that this underestimates the actual mean biomass slightly, because of the concave nature of the exponential curve. More accurate estimates could be made by dividing the year into shorter time periods for the computation, or (approximately) by using the arithmetic mean of the initial and final biomass. Paulik and Bayliff's (1967) computer programs make computations at short time intervals feasible.

TABLE 20. Model A: Computation of production. See text for details.

	Symbol	Age						Total
		1+	2+	3+	4+	5+	6+	
1. Growth rate	G	1.5000	0.5000	0.4000	0.3000	0.2000	0.1500	–
2. "X" growth rate	G_X	1.4394	0.4382	0.3367	0.2355	0.1341	0.0826	–
3. $G-G_X$	–	0.0606	0.0618	0.0633	0.0645	0.0659	0.0674	–
4. Numerical mortality rate	Z	0.7296	0.6888	0.6481	0.6074	0.5669	0.5267	–
5. Ponderal mortality rate	Z_W	0.7902	0.7506	0.7114	0.6719	0.6328	0.5941	–
6. Rate of increase in biomass	H	+0.7098	−0.2506	−0.3114	−0.3719	−0.4328	−0.4441	–
7. Initial biomass (*kg*)	B	100.0	203.8	158.4	115.9	80.0	51.9	–
8. $(e^H-1)/H$	–	1.456	0.884	0.858	0.835	0.812	0.808	–
9. Mean biomass (*kg*)	$\overline{B}$	145.6	180.1	135.9	96.8	65.0	41.9	665
10. Production ($=G\overline{B}$) (*kg*)	P	218	90	54	29	13	6	410
11. $G_X\overline{B}$ (*kg*)	–	210	79	46	23	9	3	370

TABLE 21. Model B: Computation of production.

	Symbol	Year of life						Total	Total (2+ to 6+)
		1+	2+	3+	4+	5+	6+		
1. Mean biomass	$\overline{B}$	179.1	313.4	304.1	167.8	56.2	15.9	1036	857
2. Growth rate	G	1.216	0.551	0.470	0.279	0.256	0.178	–	–
3. Production ($=G\overline{B}$)	P	218	173	143	47	14	3	598	380
4. "X" growth rate	G_X	1.216	0.528	0.438	0.254	0.250	0.178	–	–
5. $G_X\overline{B}$	–	218	165	133	43	14	3	576	358
6. "UX" growth rate	G_{UX}	–	0.362	0.404	0.244	0.247	0.178	–	–
7. $G_{UX}\overline{B}$	–	–	113	123	41	14	3	–	294

TABLE 22. Computation of production for Silver Lake ciscoes, using data of Table 1, and $Z = 0.7$.

Age	No. of fish N	Biomass B	Mean biomass $\bar{B}$	Instantaneous growth rate G	Production $P = G\bar{B}$	Using "X" growth rate	
						G_X	$G_X\bar{B}$
		kg	*kg*		*kg*		
1	10,000	116					
			136	1.24	169	1.02	139
2	4,966	159					
			132	0.62	82	0.30	40
3	2,470	108					
			83	0.33	28	0.15	13
4	1,228	62					
			48	0.28	13	0.16	8
5	611	36					
			29	0.22	6	0.16	4
6	304	21					
Total			428		298		204

calculated from Table 16. Production during ages 3+ and 4+ was 3.47 times the weight of stock at age 3, whereas the estimate using G_X was 21% lower.

There are two examples in which a "production" estimate using G_{UX} growth rates (unadjusted estimates from catch samples) can be compared with true production. In the Model B stock there was fishing from age 2+ onward, and line 7 of Table 21 gives the product of mean biomass and G_{UX}; this underestimates production at these ages by 23%. Finally, the production estimates for haddock in Table 19 are 12% lower when G_{UX} growth rates are used instead of G. These two examples illustrate the need to adjust growth estimates made from samples biassed by the selectivity of commercial fishing.

None of the above computations take into account the reproductive products discharged by a stock, which are another component of production that should be added in if a complete ecological picture is desired (Mann, 1965).

Summarizing, failure to take account of selective mortality will often mean that the biological production of a stock is substantially underestimated, and consequently also its drain on the resources of its ecosystem.

YIELD

Yields from a stock are computed as the product of rate of fishing and mean biomass each year. In the past the numerical rate of fishing F has been used, but the analysis above shows that the ponderal rate of fishing is what is needed.

Table 7 includes the values of both F and F_W for population Model B. Row 11 shows the estimates of yield that would be computed if F were used in place of F_W, compared with the true values in row 10. In total, the yield using F is 4% too small, the biggest difference being at the younger ages. The haddock example of Table 19 gives a similar result, but this is mainly because its F_W–F values were made similar to those in Model B.

BEVERTON–HOLT YIELD COMPUTATIONS

The data used to fit a von Bertalanffy growth curve to a fish population have usually or always been the observed mean lengths at successive ages. When this curve is fitted by means of a "Walford line," it can be modified very simply by plotting observed length L at age *n* against the back-calculated length L_C at age *n*–1; Fabens' statistical method of fitting could be similarly modified.

The artificial and natural stocks of Tables 1, 4, 5, and 15 above cannot be used to illustrate this because they do not conform to the von Bertalanffy relationship, but Taylor's length data for haddock (Table 17) are appropriate. The lower series of three points in Fig. 6 is a Walford plot of these data, and the points conform well to a straight line. The points in the upper line of Fig. 6 are from the same table, plotted with L_C on the abscissa. One additional point is obtained, of course, and the other points are all shifted somewhat to the left when L_C is used, increasingly so at younger ages. Thus the effect is to reduce the slope of the line, which increases the estimate of the statistic K, and may reduce or increase the estimate of L_∞. A larger K will increase the yield estimated from the yield equation of Beverton and Holt (1957, expression

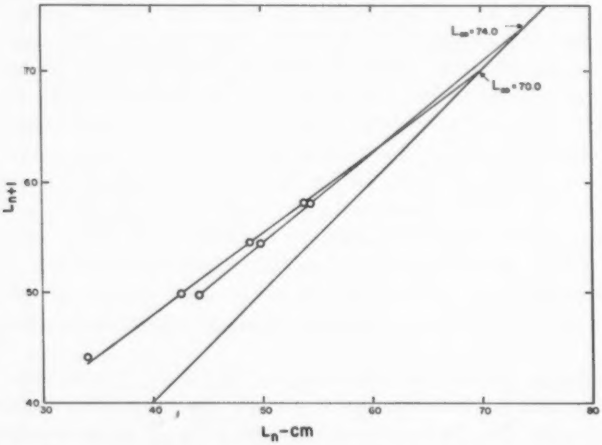

FIG. 6. *Lower points*: Walford plot of L_{n+1} against L_n for ages 3–6 of the Georges Bank haddock. *Upper points*: Plot of the same lengths at age $n+1$ against the back-calculated lengths at age *n*. For greater comparability, the left-hand point is not used in fitting the upper line.

4.4), whereas a smaller L_∞ will decrease it. Thus there is no simple rule for predicting the net effect of this change.

In any event a special study is needed to determine the effects of selective mortality upon computations of this type, and the procedure suggested in Fig. 6 may have no real usefulness. The question of whether numerical or ponderal mortality rates are required must also be considered.

SPECIAL PROBLEMS

LENGTH OF THE GROWTH YEAR AND TIME OF ANNULUS FORMATION

It has been found rather generally that as fish grow older, annuli on the hard parts of the body tend to be formed later in the season. To cite a few examples at random, this has been observed on bluegill scales by Ricker (1942), on chum and sockeye salmon scales by Bilton and Ludwig (1966), and on cod otoliths by Chugunova (1967). It means that a growth year tends to be a little longer than a calendar year. However, this makes no difference to estimates of growth rate, as long as samples are taken at some time of year when all fish either have or have not formed their annulus for that season. If this precaution is not taken, mixtures that include fish of two different year-classes may be reported as of the same age, and the growth picture will become confused as a result. Since the time of annulus formation by different individuals may extend over 2 or 3 months, and may extend into late summer in some species, the danger of mixing year-classes at this time is very real, especially among older fish. The best time for sampling is just after all fish have formed their annulus for the year, but when new or "plus" growth is still small. This minimizes any effect of the current year's selective mortality upon the growth estimate for the previous year. Alternatively, samples can be taken after the end of the growing season, among fish that stop growing during the winter, whether or not there is yet a recognizable annulus or check line on the scale.

SAMPLING ERROR

This paper has been concerned with estimating the direction and average magnitude of the various effects of selective mortality, so models have been used in which sampling error is excluded. In actual populations, of course, sampling variability exists; and this makes estimates deviate from population values and introduces irregularities into expected patterns. Sampling variances have been derived for estimates of various population statistics, but usually these depend on the realization of ideal circumstances that do not exist in the situations we have been discussing. About all an investigator can do is keep the fact of sampling variation constantly in mind.

For individual *counts* made from samples taken from large populations a good yardstick is the fact that any observed figure larger than 5 is liable to a standard deviation, from the sampling process, about equal to its own square root.

For series of observed or back-calculated *lengths*, standard deviations can and should be calculated routinely — this being no great chore in the computer age. However, such values cannot be regarded as representative of a population without examining the various biases in sampling discussed above, and making adjustments accordingly.

INACCURATE AGE DETERMINATIONS

There is general agreement among scale readers and otolith readers that perfect accuracy is rarely achieved, and that errors tend to increase as fish grow older. This has sometimes been demonstrated objectively. For example, dominant year-classes appear to become less dominant as they grow older, presumably because of misreading of older scales. Also, scale readings from fish of known age indicate that when bias in the errors exists, it is usually in the direction of reading too low.

The effects of these various situations can be determined using numerical models. Those that I have constructed lead to the following conclusions.

(1) If error in age reading is random and the same at all ages, the effect is to decrease all mean lengths. In the special case where the survival rate of the stock and the absolute increase in mean length of the fish are both the same at all ages, the decrease in the length estimate will be the same at all ages, and hence absolute length increments are not changed. In that event estimates of instantaneous rates of increase in weight are *increased* at all ages, but only very slightly.

(2) If error in age reading is random but its frequency increases with age, the above decrease in mean lengths is reduced or reversed, depending on the rate of increase in incidence of misreading. In the special case above, if the instantaneous rate of increase in percentage of misread scales with age is constant and is numerically equal to the instantaneous rate of decrease in numbers of the population, the mean lengths obtained have their true population values.

(3) If a bias toward reading ages too low is superimposed on a misreading incidence that increases with age, the average lengths obtained tend to be *larger* than in situation (2) above. If this bias is the same at all ages, and is combined with the "special case" described under (2), then the average lengths obtained are all greater than the true lengths by the same absolute amount, so that *increments* of length have their true population values.

Thus errors in scale reading can have various effects on the mean lengths and length increments obtained from a sample. They may cause either positive or negative deviations of computed mean absolute lengths from the true population values, and in either of these situations there may be either positive or a negative deviation of length *increments* from their true values. Quantitatively, the general impression obtained is that reading errors have to be gross in order to produce significant bias in either direction on estimates of growth rate.

SUMMARY

(1) Mortality selective by length within age-groups of fish is the cause of a difference (*d*) between back-calculated length at the penultimate annulus and the length at the final annulus

of fish 1 year younger. If the length at the penultimate annulus is the smaller, the difference is said to be positive, and the stock exhibits positive Lee's phenomenon.

(2) Jones (1958) has demonstrated that an initially normal length distribution remains normal, with the same standard deviation, when subjected to mortality whose instantaneous rate changes by any fixed quantity per unit of length; also that d is determined by the standard deviation (s) and by the change in mortality rate per unit of length (a) according to the relationship $d = as^2$. A new index of intensity of selection (r) is proposed that is independent of the absolute size of the fish: $r = 1.349d/s$. This index represents the difference in mean instantaneous mortality rate between the two halves of an age-group.

(3) Size-selectivity mortality also tends to decrease the mean mortality rate of a year-class as time goes on, though of course other effects are usually more important in determining the mortality rate at any given age.

(4) Size-selective mortality within an age-group gives rise to a difference between the coefficient of decline in numbers (numerical mortality rate, Z) and the coefficient of loss of weight (ponderal mortality rate, Z_w) for the age-group as a whole. If selection is positive, Z_w is larger than Z.

(5) The best estimate of instantaneous rate of increase in weight (G) in a stock comes from comparison of the mean size at the last annulus (L_2) and that at the second-last annulus (L_{1C}) among randomly sampled fish of each age. If b represents the exponent in a weight–length relationship ("year-class b" of Ricker, 1958), then:

$$G = b(\log_e L_2 - \log_e L_{1C})$$

(6) The "X-type" growth rate, which is often used, comes from a comparison of observed mean lengths at successive ages:

$$G_X = b(\log_e L_2 - \log_e L_1)$$

If selection is positive, G_X is less than G.

(7) The difference between the two growth rates above is equal to the difference between the two mortality rates:

$$G - G_X = Z_W - Z$$

This provides a method of estimating Z_W.

(8) When fishing is an appreciable cause of mortality in a stock and there is gradual recruitment to the vulnerable size range, it results in positive selective mortality. This is most easily measured if representative samples can be taken (*not* samples from the commercial catches). With ordinary rates of fishing (F between 0.3 and 1.0) and ordinary durations of the recruitment period (2–5 years for the middle 90% of a year-class), the intensity of selection will be moderate to small in magnitude (r about 0.3–0.8 for the recruitment period as a whole).

(9) Among the older age-groups selective mortality may result from declining catchability (negative selection) or from a continued increase in catchability (positive selection). However, either effect tends to be rather small because of the slow growth and great overlap in size between successive ages of the older fish.

(10) Natural selective mortality may be either positive or negative in sign. Among different species, different stocks and different ages of fish it may range from quite severe to barely detectable.

(11) Nonlinear selective mortality can cause a reduction or increase in variabliity in length of a population, but in nature such effects must be so weak as to be unrecognizable. No basis has been discovered for any causal relationship between "growth compensation" and Lee's phenomenon.

(12) Bias in sampling may favour either larger fish (so that back-calculated lengths are greater than actual), or smaller fish (so that back-calculated lengths are less than actual). Both situations produce positive Lee's phenomenon, or will intensify any positive Lee's phenomenon caused by selective mortality.

(13) Since sampling bias does not produce negative Lee's phenomenon (at any rate with likely patterns of growth and vulnerability to sampling gear), any examples observed must reflect selective mortality, provided random variability is excluded as a cause.

(14) Samples representatives of a commercial catch are characterized by both sampling bias and differential mortality at the younger ages. If these are the only source of information about population parameters, growth rates and mortality rates can still sometimes be estimated, approximately, by using adjustments obtained by comparison with the effects of selective mortality and biassed sampling in model populations

(15) Failure to recognize incompleteness of recruitment can lead to serious underestimation of mortality rates, hence overestimaticn of the increase in equilibrium catch to be obtained by increasing mean age at first capture.

(16) Computations of total yield based on numerical instead of ponderal rates of fishing are not likely to be seriously in error — probably no more than 10% low at most. This error is greatest at the younger ages. Its effect is to slightly underestimate the benefit from increasing the mean age at first capture.

(17) Computations of production in a population, if based on "X" growth rates instead of true growth rates, may be too low by up to 30% at least, though the deficiency *can* be much less. The percentage deficit tends to be greatest among the oldest age-groups.

ACKNOWLEDGMENTS

Development of the analysis in this paper has benefitted greatly from the criticisms made by colleagues in the Fisheries Research Board of Canada: Mr K. R. Allen and Dr K. S. Ketchen of the Biological Station, Nanaimo, B.C., and Dr L. M. Dickie of the Marine Ecology Laboratory, Dartmouth, N.S. Mr Erling Bakken of the latter Laboratory very kindly translated the chapter on growth in Sund's paper of 1911, including the passages quoted in Appendix 1.

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APPENDIX 1

OSKAR SUND'S DISCOVERY OF GROWTH COMPENSATION AND LEE'S PHENOMENON

Sund's 1911 paper is one of the classics of ichthyology, and it would be good to have it reprinted some time, preferably with a translation of the Norwegian text. It contains what is probably the first reference to growth compensation,* and also the first account of what later became known as Lee's phenomenon — two subjects that have generated a voluminous literature over the years.

The pertinent passages in the English summary of Sund's paper are as follows.

Concerning growth compensation (p. 407): "(2) Regarding growth in the second year, it has been shown that individuals which were small at the formation of the first winter ring grow relatively more than the larger ones (see fig. 8)."

Concerning Lee's phenomenon (p. 408): "(3) The originally small individuals will generally attain a higher age than those who grow fast in early life."

In the text Sund comments as follows about the back-calculated mean lengths shown in Table 14 above (translation by Erling Bakken):

> "Here we encounter a phenomenon parallel to what we found in 1909 during the investigation of the younger sprats (sprats used by the canning industry). The two-year-old sprats were much smaller than we would have expected from the length of the sprats of the same year-class measured the previous year. On the basis of the scale measurements, it was possible to state that this small size was not the result of a poor growth in 1908, but was due to some sprats leaving the schools of young sprats to join the schools made up of spawning sprats.
>
> "Such a school of spawning sprats is considered here. Every fish was in the process of spawning or would spawn within a short time. The two-year-olds in this school demonstrate a considerably greater length after the first period of growth (during the year of birth) than the older year-classes in the same school had at a similar age. The growth curve for the two-year-olds (1906 year-class) is steeper than that of the three oldest year-classes (1904–1902 year-classes). The three-year-old fish (1905 year-class) occupy an intermediate position."

After considering the corresponding picture of growth in weight, Sund continues as follows:

> "Now, what could be the reason for finding consistently smaller and smaller central areas in the scales, as we examine increasingly older year-classes? (From a small central area we infer a small individual size by the first winter of life.) We do not believe it is caused by any kind of bias in the catches that made up our material; the material is substantial and too much regularity is present. The explanation must necessarily be that the extremely large individuals among the young fish *die* when they have reached this species' maximum size, and usually only those individuals that begin their growth moderately, and are of a small or medium size at the end of the first growth-period, will have a chance of reaching a high age (more than 4–5 years)."

It is evident that Sund recognized both biassed sampling (among the younger fish) and selective mortality (among the older ones) as causes of positive Lee's phenomenon. He did not recognize the negative Lee's phenomenon that is present at the oldest ages in his material because of unfortunate arithmetical errors in two of the means.

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*I have not searched extensively to see whether there is an earlier account of growth compensation. Van Oosten (1929, p. 336) says that "the law of compensation in growth [was] developed by Gilbert (1914) and others."

The principal evidence that Sund presented for growth compensation is his figure 9, showing that variability in length of a group of age-2 sprats from Rosfjord was less than that of their back-calculated lengths at age 1. In his words:

> "Sprats in their second year of life are more homogeneous in size than could be expected on the basis of the large variation in size among the fry, variation which is observed both in nature and among measurements on the scales. In other words, an adjustment takes place and smooths out differences created by such factors as: variation in time of spawning, water temperature during the fry period, differences in food availability for the schools of fry, and other unknown reasons."

Sund also discussed the increase in weight among these fish. He noted that relative rate of increase in weight during the second year of life was greater among the smaller of the age-1 individuals, and concluded that this explained the contraction of variability in *length* at age 2. It is rather curious that he did not examine the rate of increase in length itself, among sprats of different sizes, and did not relate the rate of increase in weight to weight distribution at the two ages. Actually the variability in weight of these fish is greater at age 2 than at age 1. That is, the superiority in *relative* growth rate among the smaller individuals, shown in Sund's figure 8, was not great enough to prevent them from falling even farther behind the large ones in *absolute* weight. This is an example of the point mentioned on p. 506, that variability in length can decrease while variability in weight is increasing.

Unlike the Rosfjord sample, among the Langesund sprats of Table 14 length does not start to decrease in variability until age 3. It seems likely that this is the more representative situation for sprats, because there is a general tendency for calculated lengths to be a little more variable than observed lengths at any age. This is evident in Table 14. Likely causes would be a small amount of random variability in the ratio of scale radius to fish length (at any given length), or some difficulty on the part of the scale reader in locating the precise position of the annuli.

APPENDIX 2

App. Table 1. Model B: Summary of vital statistics of the fish of each length-class: B — biomass at the start of the year, kg; C — catch, in numbers; H — instantaneous rate of increase in biomass; L — length at the start of the year, mm; N — number of fish at the start of the year; Y — yield, in kg; Z — instantaneous rate of decrease in numbers. The instantaneous rate of fishing (F) is equal to Z–0.2, and the instantaneous rate of growth (G) is equal to H+Z. See App. Table 2 for details of calculations.

1	2	3	4	5	6	7	8	9	10	11	12
		Age 1+						Age 2+			
L	N	B	Z	H	L	N	B	Z	C	H	Y
62.5	2	0.00	0.2	+1.5634	112.5	2	0.02	0.2	0	+0.5092	0
67.5	11	0.03	0.2	+1.4632	117.5	9	0.15	0.2	0	+0.4819	0
72.5	49	0.19	0.2	+1.3735	122.5	40	0.74	0.2	0	+0.4573	0
77.5	166	0.77	0.2	+1.2934	127.5	136	2.82	0.2	0	+0.4339	0
82.5	440	2.47	0.2	+1.2214	132.5	360	8.38	0.2	0	+0.4123	0
87.5	919	6.16	0.2	+1.1560	137.5	752	19.56	0.2	0	+0.3922	0
92.5	1498	11.86	0.2	+1.0966	142.5	1226	35.50	0.2	0	+0.3730	0
97.5	1915	17.75	0.2	+1.0417	147.5	1568	50.31	0.2	0	+0.3556	0
102.5	1915	20.62	0.2	+0.9919	152.5	1568	55.60	0.3	135	+0.2388	6.28
107.5	1498	18.61	0.2	+0.9457	157.5	1226	47.91	0.4	202	+0.1232	10.20
112.5	919	13.08	0.2	+0.9031	162.5	752	32.28	0.5	178	+0.0082	9.72
117.5	440	7.14	0.2	+0.8635	167.5	360	16.93	0.6	108	−0.1056	6.43
122.5	166	3.05	0.2	+0.8239	172.5	136	6.96	0.7	49	−0.2191	3.12
127.5	49	1.02	0.2	+0.7927	177.5	40	2.24	0.8	17	−0.3314	1.15
132.5	11	0.26	0.2	+0.7606	182.5	9	0.55	0.9	4	−0.4437	0.31
137.5	2	0.05	0.2	+0.7306	187.5	2	0.11	1.0	1	−0.5548	0.07
Total	10000	103.06				8187	280.05		694		37.27
Mean L	100.0					150.0			161.1		

(*Continued*)

App. Table 1. Model B. Summary of vital statistics of the fish of each length-class: B — biomass at the start of the year, kg; C — catch, in numbers; H — instantaneous rate of increase in biomass; L — length at the start of the year, mm; N — number of fish at the start of the year; Y — yield, in kg; Z — instantaneous rate of decrease in numbers. The instantaneous rate of fishing (F) is equal to Z-0.2, and the instantaneous rate of growth (G) is equal to H+Z. See App. Table 2 for details of calculations.

13	14	15	16	17	18	19	20	21	22	23	24	25	26
			Age 3+							Age 4+			
L	N	B	Z	C	H	Y	L	N	B	Z	C	H	Y
142.5	1	0.03	0.2	0	+0.3730	0	172.5	1	0.06	0.6	+	-0.2709	0.02
147.5	7	0.24	0.2	0	+0.3556	0	177.5	6	0.34	0.7	2	-0.3796	0.14
152.5	33	1.16	0.2	0	+0.3388	0	182.5	27	1.63	0.8	11	-0.4883	0.77
157.5	111	4.35	0.3	10	+0.2232	0.49	187.5	82	5.43	0.9	38	-0.5958	2.86
162.5	295	12.66	0.4	49	+0.1082	2.67	192.5	198	14.10	1.0	100	-0.7036	8.10
167.5	616	28.95	0.5	146	-0.0056	8.62	197.5	374	28.79	1.1	204	-0.8108	17.75
172.5	1004	51.55	0.6	302	-0.1191	19.44	202.5	551	45.76	1.2	321	-0.9174	29.95
177.5	1284	71.79	0.7	462	-0.2314	32.04	207.5	637	56.96	1.3	392	-1.0240	39.22
182.5	1161	70.60	0.8	480	-0.3437	35.85	212.5	522	50.06	1.4	337	-1.1300	35.99
187.5	822	54.20	0.9	379	-0.4548	30.48	217.5	334	34.39	1.5	225	-1.2360	25.66
192.5	456	32.55	1.0	231	-0.5656	19.89	222.5	168	18.49	1.5	113	-1.2417	13.77
197.5	198	15.20	1.1	108	-0.6758	9.94	227.5	66	7.75	1.5	44	-1.2474	5.76
202.5	68	5.59	1.2	39	-0.7854	3.87	232.5	20	2.55	1.5	14	-1.2525	1.89
207.5	18	1.61	1.3	11	-0.8950	1.17	237.5	5	0.66	1.5	3	-1.2576	0.49
212.5	4	0.35	1.4	2	-1.0037	0.27	242.5	1	0.13	1.5	1	-1.2624	0.10
217.5	1	0.06	1.5	+	-1.1124	0.05	247.5	+	0.02	1.5	+	-1.2666	0.01
Total	6079	350.89		2218		164.78		2992	267.12		1806		182.48
Mean L	178.9			181.7				207.0			207.9		

(Continued)

App. Table 1. Model B: Summary of vital statistics of the fish of each length-class: B — biomass at the start of the year, kg; C — catch, in numbers; H — instantaneous rate of increase in biomass; L — length at the start of the year, mm; N — number of fish at the start of the year; Y — yield, in kg; Z — instantaneous rate of decrease in numbers. The instantaneous rate of fishing (F) is equal to Z–0.2, and the instantaneous rate of growth (G) is equal to H+Z. See App. Table 2 for details of calculations.

27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
Age 5+							Age 6+							Cumulative Z at age 7
L	N	B	Z	C	H	Y	L	N	B	Z	C	H	Y	
192.5	0.6	0.04	1.0	0.3	-0.7036	0.02	212.5	0.22	0.02	1.4	0.14	-1.2591	0.02	3.6
197.5	3.0	0.23	1.1	1.6	-0.8108	0.14	217.5	1.00	0.10	1.5	0.67	-1.2999	0.08	3.9
202.5	12.0	1.00	1.2	7.0	-0.9174	0.65	222.2	3.64	0.40	1.5	2.45	-1.3041	0.29	4.1
207.5	33.5	2.99	1.3	20.6	-1.0240	2.06	227.5	9.14	1.08	1.5	6.15	-1.3086	0.78	4.4
212.5	72.7	6.98	1.4	46.9	-1.1300	5.02	232.5	17.94	2.25	1.5	12.09	-1.3125	1.63	4.7
217.5	124.4	12.80	1.5	83.8	-1.2360	9.55	237.5	27.75	3.72	1.5	18.68	-1.3164	2.69	5.0
222.5	166.0	18.28	1.5	111.8	-1.2417	13.61	242.5	37.04	5.28	1.5	24.91	-1.3200	3.81	5.2
227.5	173.7	20.46	1.5	116.9	-1.2474	15.20	247.5	38.76	5.88	1.5	25.94	-1.3236	4.24	5.4
232.5	128.7	16.17	1.5	86.6	-1.2525	11.99	252.5	28.72	4.62	1.5	19.22	-1.3266	3.33	5.7
237.5	74.6	9.99	1.5	50.2	-1.2576	7.39	257.5	16.64	2.84	1.5	11.20	-1.3302	2.04	6.0
242.5	37.5	5.34	1.5	25.2	-1.2624	3.94	262.5	8.36	1.51	1.5	5.64	-1.3332	1.08	6.2
247.5	14.7	2.22	1.5	9.9	-1.2666	1.64	267.5	3.28	0.63	1.5	2.21	-1.3365	0.45	6.4
252.5	4.5	0.73	1.5	3.0	-1.2714	0.54	272.5	1.01	0.20	1.5	0.68	-1.3389	0.15	6.6
257.5	1.1	0.19	1.5	0.7	-1.2756	0.14	277.5	0.24	0.05	1.5	0.16	-1.3419	0.04	6.8
262.5	0.2	0.04	1.5	0.1	-1.2795	0.03	282.5	0.04	0.01	1.5	0.03	-1.3449	0.01	7.0
267.5	+	0.01	1.5	+	-1.2837	0.01	287.5	0.01	0.00	1.5	+	-1.3476	0.00	7.2
Total	847.2	97.47		564.6		71.93		193.79	28.60		130.17		20.62	
Mean L	225.3			225.5				244.9			244.9			

(Continued)

APP. TABLE 1. Model B: Summary of vital statistics of the fish of each length-class: B — biomass at the start of the year, kg; C — catch, in numbers; H — instantaneous rate of increase in biomass; L — length at the start of the year, mm; N — number of fish at the start of the year; Y — yield, in kg; Z — instantaneous rate of decrease in numbers. The instantaneous rate of fishing (F) is equal to Z–0.2, and the instantaneous rate of growth (G) is equal to H+Z. See App. Table 2 for details of calculations. — (*Concluded*)

42	43	44	45	46	47	48	49	50
Age 7+							Age 8+	
L	N	B	Z	C	H	Y	L	N
227.5	0.06	0.01	1.5	0.04	-1.3086	+	242.5	0.01
232.5	0.22	0.03	1.5	0.15	-1.3125	0.02	247.5	0.05
237.5	0.81	0.11	1.5	0.55	-1.3164	0.08	252.5	0.18
242.5	2.04	0.29	1.5	1.37	-1.3200	0.21	257.5	0.46
247.5	4.00	0.61	1.5	2.70	-1.3236	0.44	262.5	0.89
252.5	6.19	1.00	1.5	4.17	-1.3266	0.72	267.5	1.38
257.5	8.26	1.41	1.5	5.57	-1.3302	1.01	272.5	1.84
262.5	8.65	1.56	1.5	5.83	-1.3332	1.12	277.5	1.92
267.5	6.41	1.23	1.5	4.32	-1.3365	0.88	282.5	1.42
272.5	3.71	0.75	1.5	2.50	-1.3389	0.54	287.5	0.83
277.5	1.86	0.40	1.5	1.26	-1.3419	0.28	292.5	0.42
282.5	0.73	0.16	1.5	0.49	-1.3449	0.12	297.5	0.16
287.5	0.23	0.05	1.5	0.15	-1.3476	0.04	302.5	0.05
292.5	0.06	0.01	1.5	0.04	-1.3500	0.01	307.5	0.01
297.5	0.01	+	1.5	0.01	-1.3524	+	312.5	+
302.5	+	+	1.5	+	-1.3548	+	317.5	+
Total	43.25	7.62		29.14		5.48		9.63
Mean L	259.9			259.9				274.9

APP. TABLE 2. Model B: Details of computations of growth rate, mortality rate, production, and yield for each length-class at age 2+:

L_2, L_3 — lengths at age 2 and 3.
N_2 — number of fish at age 2.
F — instantaneous rate of fishing.
M — instantaneous natural mortality rate.
Z — instantaneous total mortality rate. $Z = F + M$.
A/Z — $A/Z = (1 - e^{-Z})/Z$. See column 4 of Appendix II of Ricker (1958).
$\overline{N}$ — average number of fish present during age 2+. $\overline{N} = N_2A/Z$.
C — catch, in numbers. $C = F\overline{N}$.
B_2 — biomass of stock at age 2.
G — instantaneous rate of growth. $G = 3(\log_e L_3 - \log_e L_2)$.
H — instantaneous rate of increase in biomass (negative values indicate decrease). $H = G - Z$.
$(e^H - 1)/H$ — for positive H, values are shown in column 5 of Appendix II of Ricker (1958); for negative H, values are in column 4.
$\overline{B}$ — average biomass of fish present during age 2+. $\overline{B} = B_2(e^H - 1)/H$.
Y — yield. $Y = F\overline{B}$.
P — production. $P = G\overline{B}$.
S — survival rate (in numbers). $S = e^{-Z}$. Values are given in column 3 of Appendix II of Ricker (1958).
N_3 — number of fish at age 3.
e^H — for positive H, values of $e^H - 1$ are shown in column 12 of Appendix II of Ricker (1958); for negative H, values of e^H are in column 3.
B_3 — biomass at age 3. $B_3 = B_2e^H$.

L_2	L_3	N_2	F	M	Z	A/Z	$\overline{N}$	C	B_2	G	H	$(e^H-1)/H$	$\overline{B}$	Y	P	S	N_3	e^H	B_3
112.5	142.5	2	0	0.2	0.2	0.9063	1	0	0.02	0.7092	+0.5092	1.303	0.03	0	0.02	0.8187	1	1.6640	0.03
117.5	147.5	9	0	0.2	0.2	0.9063	8	0	0.15	0.6819	+0.4819	1.285	0.19	0	0.13	0.8187	7	1.6192	0.24
122.5	152.5	40	0	0.2	0.2	0.9063	36	0	0.74	0.6573	+0.4573	1.268	0.94	0	0.62	0.8187	33	1.5798	1.16
127.5	157.5	136	0	0.2	0.2	0.9063	123	0	2.82	0.6339	+0.4339	1.252	3.53	0	2.24	0.8187	111	1.5433	4.35
132.5	162.5	360	0	0.2	0.2	0.9063	326	0	8.38	0.6123	+0.4123	1.238	10.38	0	6.36	0.8187	295	1.5103	12.66
137.5	167.5	752	0	0.2	0.2	0.9063	682	0	19.56	0.5922	+0.3922	1.225	23.96	0	14.19	0.8187	616	1.4803	28.95
142.5	172.5	1226	0	0.2	0.2	0.9063	1112	0	35.50	0.5730	+0.3730	1.212	43.03	0	24.66	0.8187	1004	1.4521	51.55
147.5	177.5	1568	0	0.2	0.2	0.9063	1421	0	50.31	0.5556	+0.3556	1.201	60.42	0	33.57	0.8187	1284	1.4285	71.79
152.5	182.5	1568	0.1	0.2	0.3	0.8639	1354	135	55.60	0.5388	+0.2388	1.129	62.77	6.28	33.82	0.7408	1161	1.2697	70.60
157.5	187.5	1226	0.2	0.2	0.4	0.8242	1011	202	47.91	0.5232	+0.1232	1.064	50.98	10.20	26.67	0.6703	822	1.1311	54.20
162.5	192.5	752	0.3	0.2	0.5	0.7869	592	178	32.28	0.5082	+0.0082	1.004	32.41	9.72	16.47	0.6065	456	1.0089	32.55
167.5	197.5	360	0.4	0.2	0.6	0.7520	271	108	16.93	0.4944	−0.1056	0.9490	16.06	6.43	7.94	0.5488	198	0.8998	15.20
172.5	202.5	136	0.5	0.2	0.7	0.7191	98	49	6.96	0.4809	−0.2191	0.8980	6.25	3.12	3.01	0.4966	68	0.8032	5.59
177.5	207.5	40	0.6	0.2	0.8	0.6883	28	17	2.24	0.4686	−0.3314	0.8511	1.91	1.15	0.90	0.4493	18	0.7179	1.61
182.5	212.5	9	0.7	0.2	0.9	0.6594	6	4	0.55	0.4563	−0.4437	0.8076	0.44	0.31	0.20	0.4066	4	0.6416	0.35
187.5	217.5	2	0.8	0.2	1.0	0.6321	1	1	0.11	0.4452	−0.5548	0.7675	0.08	0.07	0.04	0.3679	1	0.5800	0.06
Total		8187					7070	694	280.05				313.37	37.27	170.84		6079		350.89
Mean L		150.0						161.1											

Polyteny and Size Variation in the Copepod *Pseudocalanus* from Two Semi-Landlocked Fiords on Baffin Island[1,2]

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WOODS, SUSAN M. 1969. *Polyteny and size variation in the copepod Pseudocalanus from two semi-landlocked fiords on Baffin Island.* J. Fish. Res. Bd. Canada 26: 543–556.

Two forms of the copepod *Pseudocalanus*, which differ only in size, coexist in two semi-landlocked fiords on Baffin Island. The large form possesses the same number of chromosomes as the small but its chromosomes are conspicuously larger and contain about seven times as much DNA. Due to polyteny, the large form has a greater cell size and a slower development rate than the small form. The large form, having an essentially annual life cycle, matures later than the small form. Two generations of the small form may be produced in a summer with only the first reaching maturity. As the fiord waters are warmer, the small form is smaller and develops faster than its counterpart in nearby seas. The large form may represent an evolutionary attempt to restore normal arctic size and development rate in the fiords. In the cold waters of the sea, the slow development rate of the large form might lead to an excessively long life cycle, perhaps biennial. This may explain the apparent absence of the large form outside the two fiords. The polytene form may be a new species but, as the taxonomy of the genus is indefinite, a new name is deferred.

Received October 1, 1968

INTRODUCTION

SEASONAL SIZE VARIATIONS within local populations of the copepod genus *Pseudocalanus* have recently been studied in relation to temperature and food differences (Deevey, 1960; McLaren, 1963, 1965b). Collections taken in 1957 by McLaren (1965b) from Oğac Lake, a warm semilandlocked fiord on Baffin Island at 62°52′N and 67°21′W, however, revealed size variation within a population of *Pseudocalanus* exposed to similar environmental influences. This situation was found later, in 1964, to occur in *Pseudocalanus* samples collected from the semi-landlocked head of Winton Bay on the east coast of Baffin Island at 63°24′N and 64°39′W.

The larger form carried eggs of a significantly larger size than those of the smaller form. No mention of such a large-egged form occurring elsewhere has been found in the literature. McLaren (1965b) considered it possible that these large animals were polyploid, but this hypothesis was not examined further at that time. Therefore, a comparative study of the differently sized forms, their chromosomes, and their nuclear DNA contents has been carried out.

The morphological features of both forms, excluding size, coincide with the detailed description of *Pseudocalanus gracilis* by Sars (1903). However, it is uncertain whether the genus *Pseudocalanus* is comprised of three distinct

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[1] The fifth paper in a series of studies on Ogac Lake.

[2] Based on a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science from McGill University, Montreal, Que.

Printed in Canada

species, *P. elongatus* Boeck, *P. gracilis* Sars, and *P. major* Sars (see Brodsky, 1950; Sars, 1903) or whether all these species are actually synonymous with *P. minutus* (Krøyer) as assumed by some authors (With, 1915; Farran, 1951; Fontaine, 1955; Østvedt, 1955). Because of this uncertainty in taxonomy and also the existence of the unclassified large-egged form, the animals discussed here will be referred to by the generic name only.

MATERIALS AND METHODS

Sampling Methods

Plankton hauls were taken during 1952, 1957, 1962, and 1965 from Ogac Lake and during 1964 from Winton Bay. The material from Ogac Lake in 1957 and 1962 was collected and analysed by I. A. McLaren according to methods described elsewhere (McLaren, 1969). Briefly, parallel vertical hauls were taken usually from anoxic depths with fine-mesh (no. 20) and coarse-mesh (no. 6) nets. Laboratory sampling allowed conversion of counts between the two nets. The efficiency of the no. 6 net was estimated for the 1957 samples and use of a Clarke-Bumpus quantitative sampler in 1962 allowed direct calculations of numbers per square metre. A 0.5-m, no. 6 net used in 1962 was found to be 100% efficient.

Similar methods were used to capture and analyse the material from Winton Bay in 1964 and Ogac Lake in 1965. Quantitative estimates were based on the assumption that the 0.5-m, no. 6 net was 100% efficient. Only a fine-mesh net was used in Winton Bay on Aug. 3, 1964; the sample can accordingly be used only for information on the relative abundance of stages.

Unfortunately, only samples from fine-mesh (no. 18) net hauls were available from Ogac Lake in 1952. Numbers were, therefore, calculated assuming this net to be 100% efficient for all stages. It is possible that this efficiency was, in fact, almost achieved in the phytoplankton-poor waters during August when the samples used here were collected.

Depending upon the abundance of the copepodites in the complete haul, the counts of the copepodite stages were made on either the whole sample or a random subsample. Egg-bearing females were removed from the whole sample to avoid detaching the eggs in the act of subsampling. The sizes of the subsamples varied but they were usually 10% or greater. Counts of the naupliar stages were made from random subsamples of 10–20%.

The egg diameters were determined from the average of the maximum and minimum diameters of each egg if it was not perfectly spherical. In order to compare the adult female cephalothorax lengths and the egg diameters, only those eggs still attached to the females were measured.

Determination of Volume Ratios

Comparisons of length and mean width of the cephalothorax of *Pseudocalanus* (McLaren, 1965b) imply that volume is proportional to length to the power of 3.32. This function was used to estimate volume ratios of stage I copepodites and adult females. The volumes of the small and large eggs were calculated from the mean diameters, assuming the eggs to be spherical.

To estimate the volume ratio of the nuclei of the small and large forms, 10 adult females of each form were stained in haematoxylin and squashed in Permount on separate slides. Like other organisms, copepods may exhibit somatic ploidy (Stich, 1962) and therefore only a single type of nucleus — spherical and densely staining — was measured. The diameters of 10 such nuclei in each female were measured and the mean diameter of the two forms was calculated. The relative volumes were calculated assuming the diameters to be those of two spheres.

Chromosome Staining

At the time of studies by I. A. McLaren on the development rate of copepod eggs (McLaren, 1966), fresh eggs were secured for chromosome study. The eggs or early embryos were squashed in aceto–orcein stain. The squashes were then covered and the slides sealed. Only the chromosomes of eggs at the metaphase stage of division were used for comparison.

Staining and Cytophotometric Analysis of Nuclear DNA

Cytophotometric analysis has been employed to study the relative amount of nuclear DNA in eggs of the small and large forms from formalin-preserved plankton samples taken at

Ogac Lake in 1965. Eggs of each form were treated concurrently to avoid introduction of variants due to the staining procedure. The eggs were deformalinized (Lotho and Vaz Ferriera, cited by Davenport, 1960) by washing in distilled water for 15 min and soaking in two 24-hr changes of 20% aqueous chloral hydrate. They were then washed for 15 min in distilled water before staining.

The Feulgen reaction (de Tomasi, 1936) was employed as a measure of relative amount of nuclear DNA. The specificity and stoichiometry of this reaction have been validated by Stowell (1946), Swift (1953, 1955) and Leuchtenberger (1958). After deformalinization, the eggs were hydrated in 70% alcohol for 2 hr, 50% alcohol for 1 hr, and 30% alcohol for 1 hr, then kept in distilled water for 12 hr. They were rinsed in cold 1 N HCl for 2 min and then hydrolysed in 1 N HCl for 9 min at 60 C. After hydrolysis, the eggs were rinsed in cold 1 N HCl for 2 min and washed in three 10-min changes of distilled water. The eggs were next treated with Schiff's reagent for 45 min. Several nonhydrolysed eggs served as a control. The eggs were removed from the reagent and were transferred through three 10-min changes of sulphurous acid rinse. They were then washed in three 10-min changes of distilled water, dehydrated in absolute alcohol for 10 min, and cleared in alcohol–xylene (1:1). Squash preparations of these eggs were made and mounted on separate slides in oil of refractive index (R. P. Cargille Inc.) to match the nuclear refractive index (small form, 1.580; large form, 1.592).

Cytophotometric measurements were made on these squash preparations. For the theoretical background and details regarding equipment, the reader is referred to the original papers (Swift and Rasch, 1956; Pollister and Ornstein, 1955, 1959; Mendelsohn, 1958a). The cytophotometric technique used was the aperture method, and all measurements were made by the two-wavelength method (Ornstein, 1952; Patau, 1953).

Absorption spectrum measurements were taken 10 mμ apart; the maximum absorption at $\lambda_{570\,m\mu}$ was selected as one wavelength. The second wavelength was estimated by linear regression (Garcia, 1962) and ultimately established by trial and error at $\lambda_{500\,m\mu}$. Subsequently, transmissions at $\lambda_{570\,m\mu}$ and $\lambda_{500\,m\mu}$ were used as a measure of the amount of nuclear DNA per cell.

Duplicate readings were taken of 10 nuclei in five eggs of each of the small and large forms at the 32-cell stage. The average extinction for each field was obtained from Mendelsohn's Tables (Mendelsohn, 1958b). Since the entire nucleus was included in the photometric field, the total amount of chromatophore per nucleus was estimated by multiplying the average extinction by the area of the photometric field (small, 523.0 μ^2; large, 2084.6 μ^2; see Table 1).

ENVIRONMENT AND ITS POSSIBLE INFLUENCES

The physical and chemical characteristics of Ogac Lake have been described in detail by McLaren (1967). The lake lies at the head of an inlet on the southwest shore of Frobisher Bay. It is divided into three basins, which are anoxic below 25–32 m. The surface waters are fresh and the deeper waters are only slightly brackish (up to 27‰). The lake is much warmer than the sea outside; at the height of summer warming in 1957 the upper 30 m of the middle basin (from which the samples in the present paper were taken) had a mean temperature of about 7.5 C, compared with 0.5 C in the sea outside. The head of Winton Bay, which is situated on the southwest shore of Robinson Sound, is similar to Ogac Lake in many of its physical aspects (McLaren, 1967). It is divided into two basins which are anoxic below 31–32 m. Since it receives more tidal water, it is more saline and cooler than Ogac Lake (up to 32‰ and with a mean temperature in the upper 30 m of 1.7 C on August 6, 1964). Both Ogac Lake and Winton Bay are extreme examples of the fiord condition as described by Dunbar (1958).

The warmer temperatures of these lakes are of particular significance in this study. Deevey (1960) showed that the size of copepods is strongly correlated with the temperature of the environment and the estimated amounts

TABLE 1. Photometric measurements of DNA–Feulgen complex on nuclei of five small and five large eggs corresponding to the 32-cell stage. Amount of chromatophore is determined as an average of duplicate readings of 10 nuclei each per egg.

	Average extinction ($\bar{\mu} \pm \sigma$)	Photometric area (μ^2)	Total amount chromatophore
Small eggs	.122±.025	523.0	63.8
	.138±.021		72.2
	.141±.036		73.7
	.115±.012		60.2
	.146±.016		76.4
Amount DNA/nucleus	.132±.022		69.0
Large eggs	.241±.030	2084.6	502.4
	.233±.029		485.7
	.279±.030		581.6
	.202±.026		421.1
	.238±.012		496.1
Amount DNA/nucleus	.239±.035		498.2

of food, but that the degree of dependence upon these factors varies with the geographical area, especially the temperature range of the species being considered. McLaren (1963) has demonstrated that for some groups of poikilotherms, including calanoid copepods, size at any stage of development is a function of temperature alone, although lack of food may thwart growth and development and thus affect size indirectly. The size–temperature curve given by McLaren (1965b) for *Pseudocalanus* in the eastern Canadian Arctic showed a rather steep inverse size–temperature relationship.

Of the six geographical areas studied by McLaren (1965b), only in Loch Striven was egg size found to be negatively correlated with temperature and positively correlated with the mean female length. Even then, although the female length varied about 35%, egg size varied only 7%.

MORPHOLOGY OF THE LARGE AND SMALL FORMS OF *PSEUDOCALANUS*

Two forms of *Pseudocalanus*, which differed only in size, were found coexisting in both Ogac Lake (illustrated and discussed briefly by McLaren, 1965b) and Winton Bay. The morphological features were similar to those attributed to *P. gracilis* by Sars (1903). The head of the adult copepodite was slightly tapered. The first legs of the adult female were smaller than the other legs and bore one long seta on the inner side of each basipod. The endopod and exopod consisted of one and three segments respectively. The basal segments of the asymmetrical fifth pair of legs of the adult male were approximately equal in length. The pointed terminal segment of the right leg, which consisted of three segments, was about equal in length to the basipod. The left leg was longer than the right and, including the basipod, consisted of five segments. The terminal segment of the left leg was tipped with a slender spinule. The authors who distinguished several species of *Pseudocalanus* (Brodsky, 1950; Sars, 1903) employed the fifth pair of legs in the adult male and the first pair in the adult female as two of the principal distinguishing features of each species. The respective appendages showing the similarity of the large and small forms are shown in Fig. 1 and 2.

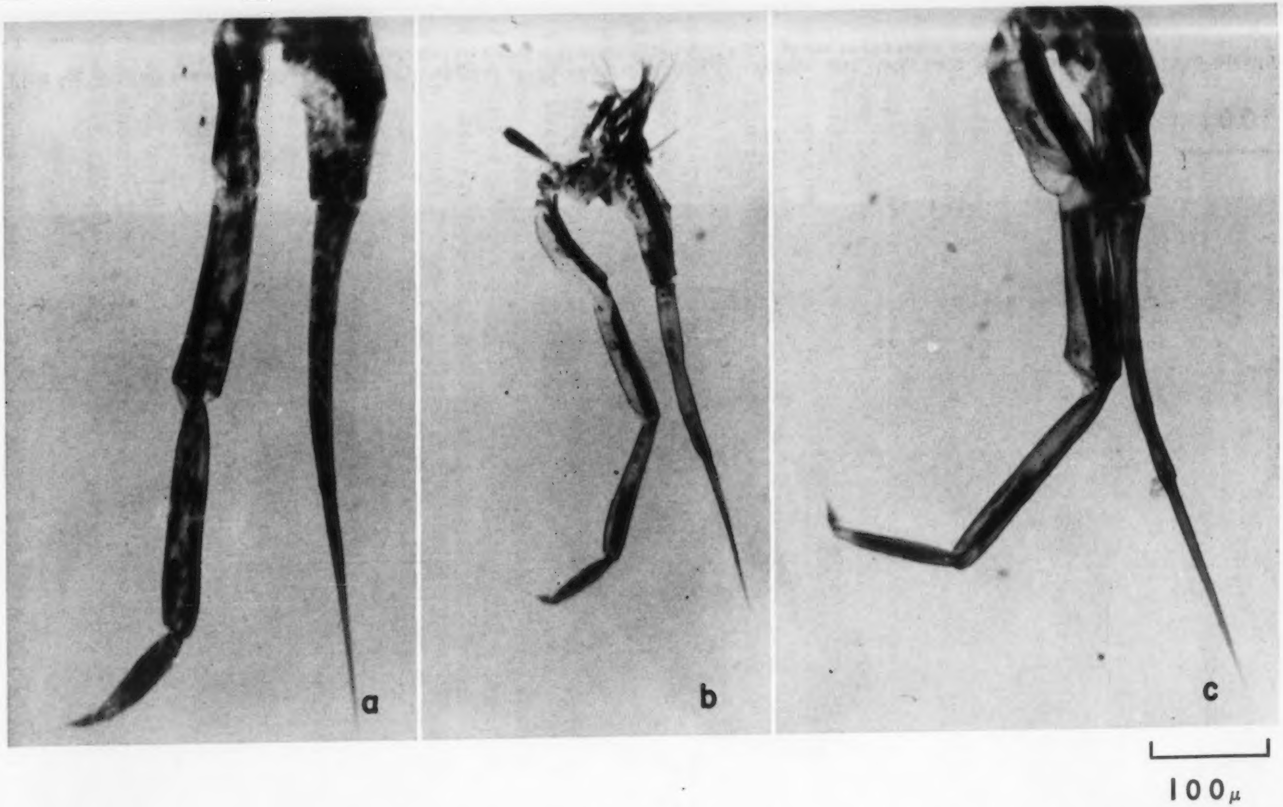

FIG. 1. Fifth leg of adult males (with cephalothorax lengths) of *Pseudocalanus* from (*a*) Winton Bay (large form = 1090 μ), (*b*) Winton Bay (small form = 688 μ), and (*c*) western Hudson Strait (1097 μ). All are to the same scale.

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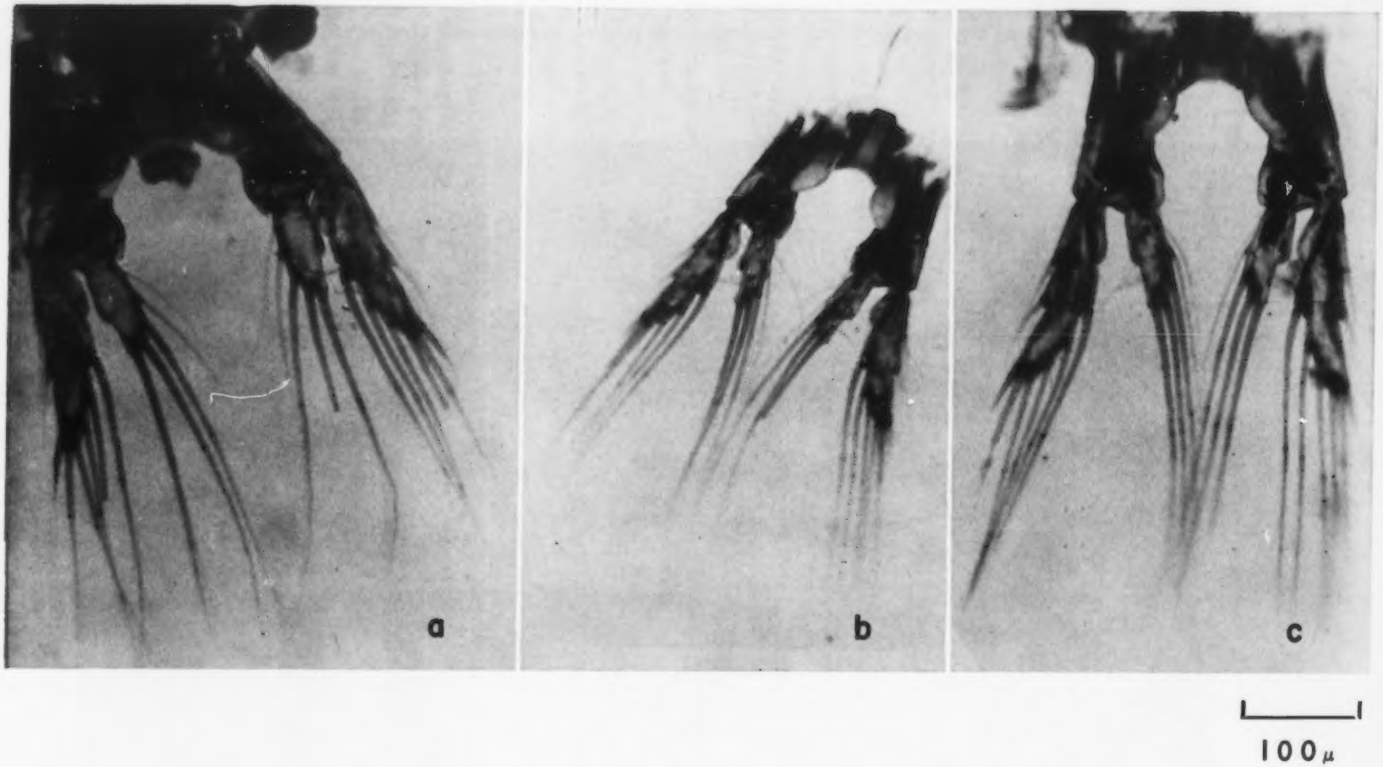


FIG. 2. First leg of adult females (with cephalothorax lengths) of *Pseudocalanus* from (*a*) Winton Bay (large form = 1215 μ), (*b*) Ogac Lake (small form = 889 μ), and (*c*) western Hudson Strait (1264 μ.) All are to the same scale.

BODY AND EGG SIZE OF THE TWO FORMS

All copepodites and nauplii contained in complete samples or subsamples collected from Winton Bay in 1964 and Ogac Lake in 1965 were measured either for cephalothorax length in the case of the copepodites or for cephalosome length in the naupliar stages. The frequencies and size distributions recorded from one collection taken from Ogac Lake on August 6, 1965, and one from Winton Bay on August 15, 1964, are presented in Fig. 3 and 4.

The size ranges of all stages from first nauplius to adults for both Ogac Lake and Winton Bay appear to be bimodal. The distribution of sizes obtained in two samples was tested for the significance of the difference between the two means and the difference was found to be significant for each stage at $P < 0.05$ (Woods, MS, 1967).

Nauplii of the large and small form were hatched from eggs collected from Ogac Lake in 1965 and kept at the same temperature after collection (ca. 5 C); one of each is shown in Fig. 5. Clearly, then, the size differences were not environmentally induced.

Both size groups appearing in the Winton Bay collections averaged larger than the comparable groups in Ogac Lake. The difference between the means was tested and in a slight majority of both the naupliar and the copepodite stages was found to be significant at $P < 0.05$ (Woods, MS, 1967). Since body size in *Pseudocalanus* was negatively correlated with temperature (McLaren, 1965b) the cooler waters of Winton Bay were assumed to be responsible for the larger body size there.

In addition to the difference in body size of the two forms, the eggs borne by the large form were conspicuously larger than those of the small form. The mean diameters of eggs are plotted against the cephalothorax length of the females bearing the eggs in hauls from Winton Bay in 1964, Ogac Lake in 1965, and Frobisher Bay in 1965 (Fig. 6).

Two distinct size groups appeared in the lakes but a few large individuals carried eggs of intermediate size (Fig. 6a, b). McLaren (1969) found that numbers of large *Pseudocalanus* entered Ogac Lake at times of the highest tides but did not appear to survive long and were presumably ill-adapted to the sudden environmental change. The body size of these outside animals, which averaged one third longer than the small fiord form (McLaren, 1965b), was presumably due to the colder temperature prevalent in Frobisher Bay. It is probable, therefore, that the large specimens bearing small eggs had recently come into the lakes from outside. This is concordant with Fig. 6, which shows that their eggs were comparable in size with those from Frobisher Bay (cf. Fig. 6a, b with Fig. 6c). Eggs from Frobisher Bay (Fig. 6c) averaged slightly, but significantly ($0.05 > P > 0.01$), larger than those of the small form from Ogac Lake, this presumably being due to the cooler waters of the Bay.

CHROMOSOMES

It seems clear that neither food nor temperature could cause the size bimodalism of the indigenous populations of *Pseudocalanus* in the two landlocked fiords as these animals experienced similar environmental influences.

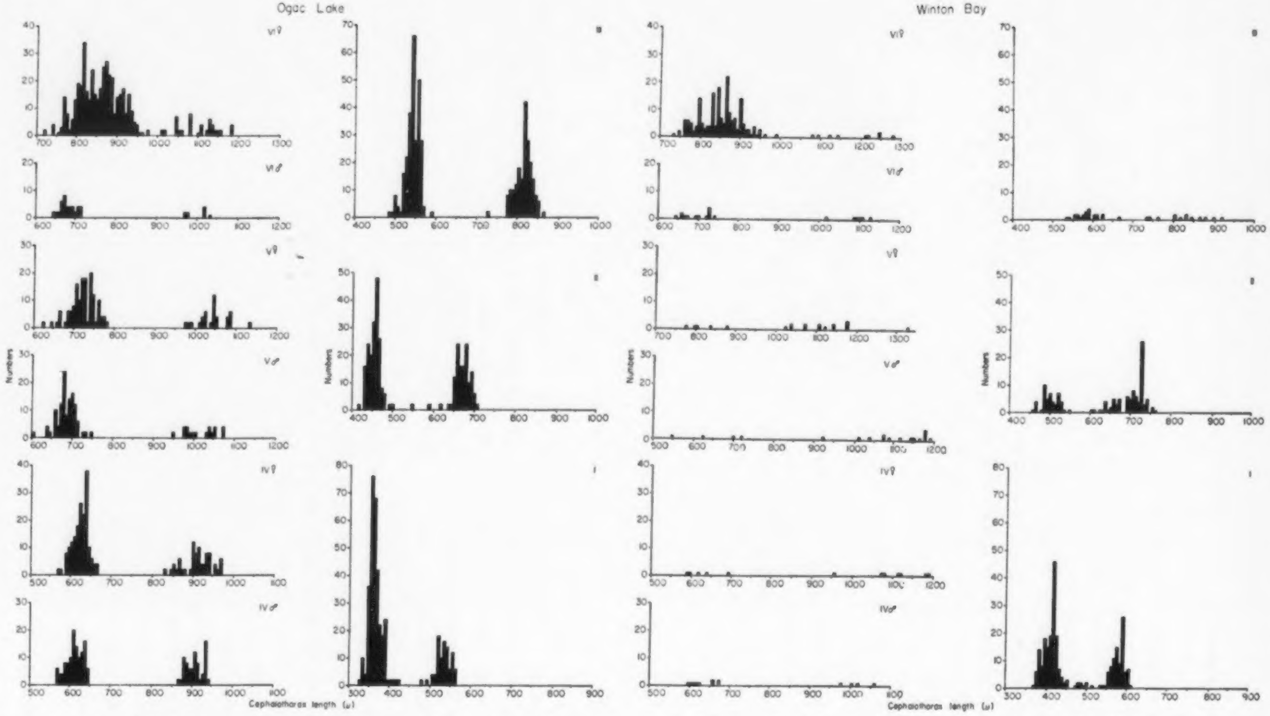
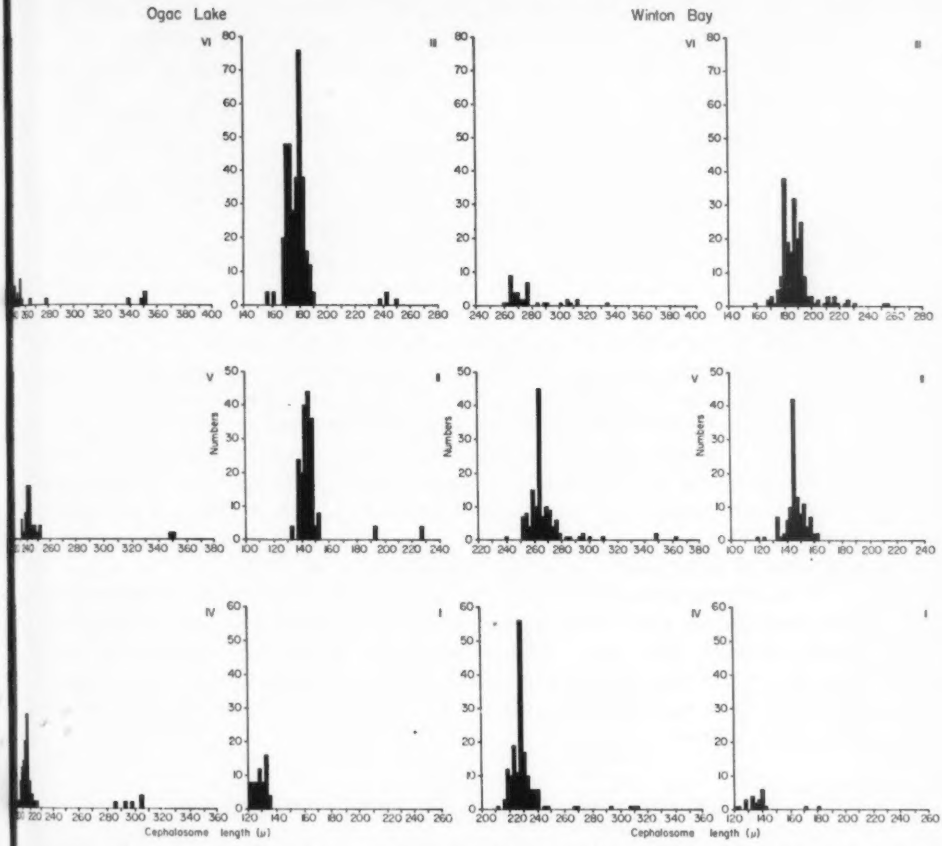


FIG. 3. Size distribution of copepodite stages I–VI inclusive from Ogac Lake (August 6, 1965) and Winton Bay (August 15, 1964). Results are determined from total sample.



Size distribution of nauplius stages I–VI inclusive from Ogac Lake (August 6, 1965) and Winton Bay (August 15, 1964). Results are determined from $\frac{1}{10}$ of total sample.

McLaren (1965b) considered it possible that the large forms could be polyploids such as those which were discovered in *Calanus finmarchicus* (Harding and Marshall, 1955). Aceto–orcein squash preparations of fresh egg sacs revealed that the large forms in Ogac Lake possessed the normal calanoid chromosome complement of $n = 16$ (Marshall and Orr, 1955) as did the small form (Fig. 7). Two eggs only of one of the large females were found to have a chromosome complement of $n = 17$ (Fig. 7b). This might have been caused by the phenomenon of nondisjunction, where pairs of chromosomes failed to separate at meiosis (Dawson, 1962).

The chromosomes of the large form, however, were noticeably larger than those of the small form and also larger than those found in fresh material collected at Frobisher, N.W.T., Halifax, N.S., and Millport, Scotland. Formalin-preserved material from Winton Bay was available for staining but the development of the embryos was too advanced to allow a detailed photograph of the chromosomes.

NUCLEAR DNA CONTENT

An important factor in the determination of chromosome size is the occurrence of polyteny, (Hughes-Schrader and Schrader, 1956) in which a chromosome endoreplicates simultaneously a number of times and, instead of separating, the daughter strands remain together forming a many-threaded polytenic cable (Herskowitz, 1962; Altenburg, 1957). Since DNA is ordinarily restricted to the chromosomes, as chromosome size increases with ascending levels of polyteny the nuclear DNA content increases proportionally (see Hughes-Schrader and Schrader, 1956; Kurnick and Herskowitz, 1952).

Since the DNA content in the resting nucleus remains constant (Darlington, 1955) a cytophotometric analysis was carried out on the Feulgen-stained interphase nuclei of the small and large forms. Although the Feulgen test cannot by itself establish the absolute amount of nuclear DNA, if the differences in DNA content are sufficiently large, the test does supply accurate estimates of the relative amounts (Leuchtenberger, 1954).

The average extinction values for each series of photometric measurements were analysed by the chi-square test and were found to have a normal distribution (Woods, MS, 1967). The results of the photometric analysis showed that the ratio of the relative amounts of DNA per nucleus in the large form to the small form was approximately 7:1 (Table 1), which seems safely attributable to polyteny.

EFFECTS OF DNA ON SIZE AND DEVELOPMENT RATE

Mirsky and Ris (1950) stated that "in general...the greater the DNA content, the larger the cell." Commoner (1964) demonstrated that in bacteria the cellular DNA content was directly related to the cell volume and in various vertebrate erythrocytes the relationship was directly proportional. Furthermore, since overall cell size is generally inversely related to the metabolic rate, the characteristic rate of oxidative metabolism of a species is inversely related to the DNA content. These relationships have also been discussed by McLaren (1965a) and Stebbins (1966). In addition, nuclear volume may be positively related to the length of the mitotic cycle (Van't Hoff and Sparrow, cited by Stebbins, 1966). Therefore, an increase in the amount of DNA should result in an increase in the cell volume but a decrease in the metabolic and division rates. Since copepods show determinate growth and probably determinate cell number (McLaren, 1965b), an increase in the amount of DNA would be expected to increase the size and to reduce the development rate of the entire animal.

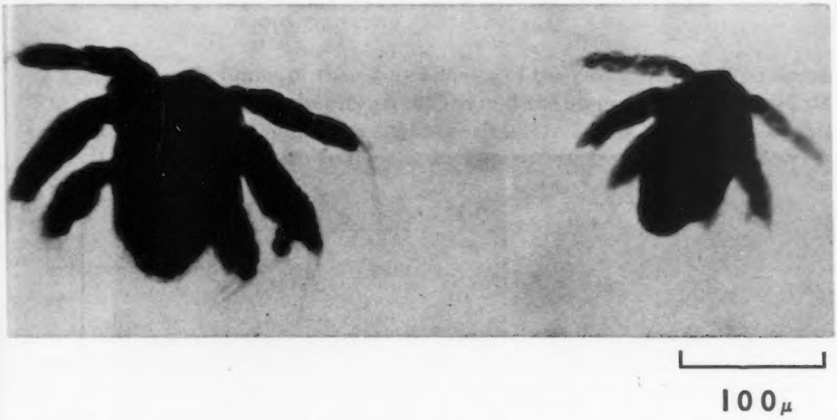


FIG. 5. Nauplius stage I hatched from adult ♀♀ from Ogac Lake with nauplius cephalosome length and female cephalothorax length: (*left*) large form (nauplius = 168 μ; ♀ = 1069 μ); (*right*) small form (nauplius = 130 μ; ♀ = 903 μ). Both are to the same scale.

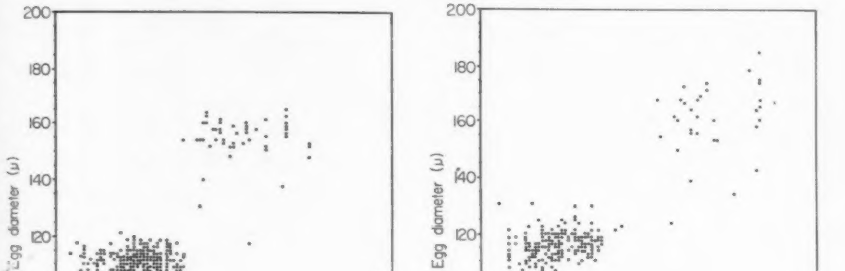


FIG. 6. Comparisons of adult female cephalothorax lengths and diameters of the attached eggs of *Pseudocalanus* from (*a*) Winton Bay, 1964; (*b*) Ogac Lake, 1965; and (*c*) Frobisher, 1965.

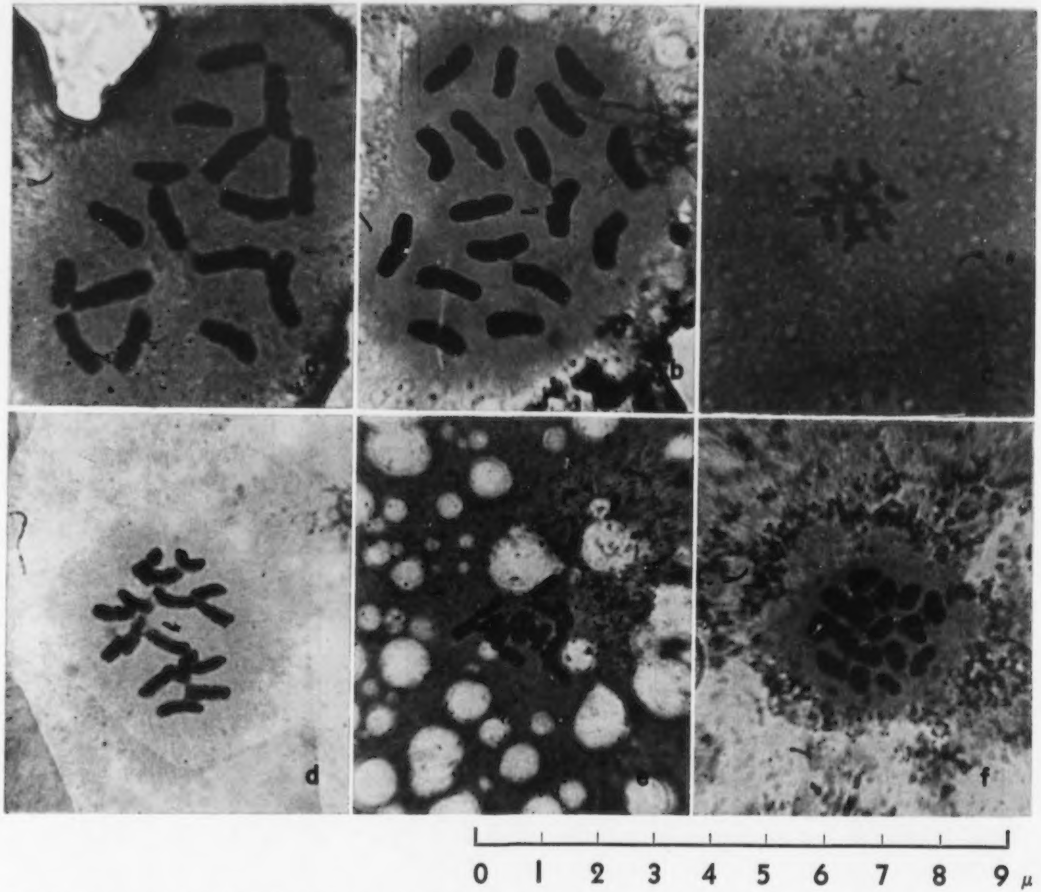


FIG. 7. Aceto-orcein stained haploid sets of metaphase chromosomes from fresh eggs of *Pseudocalanus* (*a*) the large form from Ogac Lake; (*b*) the large form from Ogac Lake with $n = 17$; and of *Pseudocalanus minutus* from (*c*) Ogac Lake; (*d*) Frobisher, N.W.T.; (*e*) Halifax, N.S.; and (*f*) Millport, Scotland. All are to the same scale.

The relative volumes of the adult females of the two forms were compared along with the volumes of their eggs, nuclei, and the stage I copepodites (Table 2). The ratios of these volumes were approximately 3:1 as shown also by McLaren (1965b). Departures from this ratio may represent slightly different environmental influences on the two forms. Therefore, since the relative nuclear DNA contents of embryos of the two forms of *Pseudocalanus* are in the proportion of 7:1, the DNA content is directly related to the volumes of eggs and older stages, but the relationship is not directly proportional. However, it may be possible that the DNA ratio of somatic cells of the large and small forms is closer to 3:1, as chromatin diminution, presumably involving loss of DNA, is known to occur during early embryogenesis of some copepods (Beermann, 1959). This possibility deserves future examination.

TABLE 2. Comparisons of sizes of the large and small forms of *Pseudocalanus* from Ogac Lake, 1965, and Winton Bay, 1964. Values are means and standard errors.

	Large form (μ)	Small form (μ)	Volume ratio
Ogac Lake			
Egg diam	158.71±0.70	110.23±0.19	2.98±0.04
Nucleus diam	5.19±0.07	3.53±0.03	3.16±0.15
♀ cephalothorax length	1089.37±3.97	851.12±0.89	2.27±0.03
Stage I copepodite length	532.40±1.33	362.04±0.94	3.60±0.04
Winton Bay			
Egg diam	162.46±0.60	116.04±0.32	2.74±0.04
Nucleus diam	5.04±0.04	3.54±0.04	2.77±0.12
♀ cephalothorax length	1159.27±4.39	840.77±0.69	2.91±0.04
Stage I copepodite length	558.00±0.83	398.41±0.35	3.06±0.02

McLaren (1965b) investigated the development rates from field samples of the small and large forms in Ogac Lake and showed that the mean rate in the small form was significantly greater at 0.42 stages per day than in the large form at 0.28 stages per day. Later, he was able to show experimentally that eggs of the small form developed about 1.7 times as fast at any temperature (McLaren, 1966).

LIFE CYCLE OF THE LARGE FORM

Sufficient material, from the middle basin of Ogac Lake in 1962, is available to outline the life history of the large form (Fig. 8); large nauplii were not separated in analysing the samples from 1957; and collections from other years were made only during brief periods in summer.

Copepodites and adults in the middle basin at the beginning of June must have overwintered from the previous season. The adults of this generation (all females, designated as G_{1961a} in Fig. 8) gave rise to nauplii of the

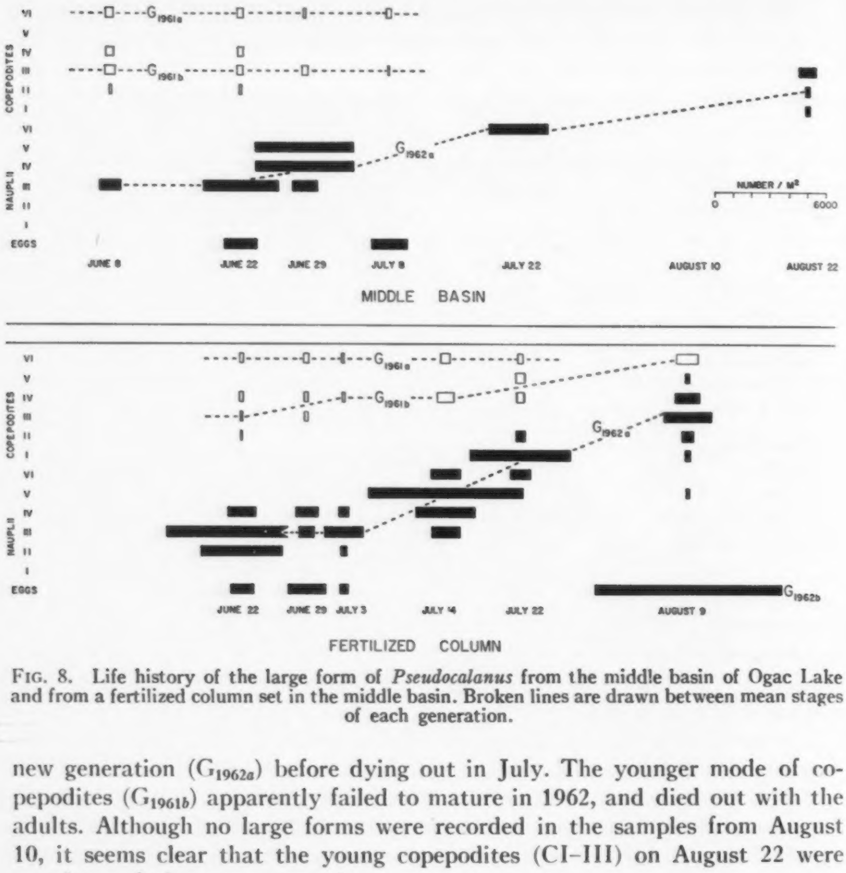


FIG. 8. Life history of the large form of *Pseudocalanus* from the middle basin of Ogac Lake and from a fertilized column set in the middle basin. Broken lines are drawn between mean stages of each generation.

new generation (G_{1962a}) before dying out in July. The younger mode of copepodites (G_{1961b}) apparently failed to mature in 1962, and died out with the adults. Although no large forms were recorded in the samples from August 10, it seems clear that the young copepodites (CI–III) on August 22 were members of the new generation.

The picture is much clearer in the results obtained from fertilized, food-rich polyethylene columns set between the anoxic depths and the fresh surface of the middle basin in 1962 (see McLaren (1969) for description of experiment and sampling methods). Here survival of G_{1962a} was greater, and the overwintered copepodites (G_{1961b}) apparently matured, as adult males (which are very short-lived) appeared for the first time in samples from August 9. The burst of eggs on August 9 may have been produced by the newly matured females of G_{1961b}, and perhaps would have developed as G_{1962b}.

Available estimates of numbers of copepodites and adults suggest that similar annual life cycles prevailed in Ogac Lake in other years and also in Winton Bay (Table 3). In 1952, 1957, 1962, and 1965 a distinct peak at CIII was present in early to mid-August. In Winton Bay in 1964, maturation of older copepodites (as indicated by the presence of adult males) and development of the apparently new generation from a peak at CI–III occurred between August 3 and August 28.

TABLE 3. Estimated numbers of copepodites of the large form of *Pseudocalanus* per square meter, in the middle basin of Ogac Lake and the outer basin of Winton Bay in all available samples from August of 5 years. Calculated as discussed in the text.

Locality and date	No. at each copepodite stage per m^2						Total no. as % of no. of copepodites of small form
	I	II	III	IV	V	VI	
Ogac Lake							
1952 Aug. 7[a]	10	70	50	80	60	20	3.0
" 12[a]	10	30	50	10			1.7
1957 " 3	630				400	1400	2.5
" 17		180	1550	260	200		4.0
" 31	150					120	1.0
1962 " 10							0.0
" 22	220	220	880				1.0
1965 " 6	1330	1870	2780	2350	1130	710	36.5
Winton Bay							
1964 Aug. 3[a]	3150	30	10	310	1750	240	338.9
" 7	1240	110	60	10	100	450	20.4
" 15	500	460	70	60	150	50	55.8
" 28	90	2500	2040	180	890	500	23.1

[a] Estimates probably low, since only less efficient fine-mesh nets were used.

The life cycle of the large form of *Pseudocalanus* of Ogac Lake differs from that of the small form, in which all the overwintered generation matures rapidly in June and the first broods of the new generation may mature, breed, and die out in summer (McLaren, 1969). The retarded maturation of the old generation and slow progress of the new generation of the large form are in keeping with its slower development rate.

DISCUSSION

The polytenic nature of the large form of *Pseudocalanus* may be taken as established. Omitting considerations of chromosome structure, genetic redundancy, and other such problems, there remain the questions of the systematic status of the large form, and why these animals should occur in two warmer, semilandlocked fiords and not apparently in the sea outside.

The apparent absence of intermediates suggests that the two size forms are reproductively isolated; possibly the differences in chromosomes would lead to hybrid malfunctions. Nuclear DNA content has been taken as a constant characteristic of a species (Mirsky and Ris, 1949, 1950), and Hughes-Schrader (1951, 1953) demonstrated that, in the morphologically similar species of the mantid genus *Liturgousa*, the amount of nuclear DNA could be employed as a character in considering systematic relationships. On these precedents the polytene form of *Pseudocalanus* could be described as a new species. However, as the taxonomy of the genus *Pseudocalanus* is still indefinite (see Introduction), it seems best to defer a name. Furthermore, it is quite possible that the polytene form has arisen independently from the ordinary form in Ogac Lake and Winton Bay, and that slight differences in degree of polyteny are involved in the two localities. This obviously raises conceptual difficulties for taxonomic analysis.

It is a reasonable assumption that the greater the amount of DNA, the more complex the organism may be, and, consequently, the greater the variation possible in its adaptability (Herskowitz, 1962; Stebbins, 1966). However, this can only be a long-term value, and the polytenic *Pseudocalanus* did not appear to differ from the small form in ways unrelated to size. There are large differences from year to year in the numbers of the large form relative to the small one in Ogac Lake, especially dates on which the large form was at about the same stage of development with a peak of numbers at CII-III (Table 3). This is in itself evidence that the two forms are differently adapted to conditions in the lake, which is not surprising in view of their different life cycles. In the fiord the small form in a sense may "waste" much of its reproductive effort, since early broods matured and produced an unsuccessful second generation in the summer (McLaren, 1969). Under these circumstances, there should be selective pressure for maturation later in the summer, which might be thwarted by the lack of complete genetic isolation from the *Pseudocalanus* living outside the landlocked fiords. The large form may therefore represent an evolutionary attempt to restore normal arctic size and development rates in the warm waters of Ogac Lake and Winton Bay. It is also possible that large size allows a greater range of food choice (Brooks and Dodson, 1965).

The apparent absence of the polytenic form in the sea outside may also be related to its slower development rate. The life cycle of the small form in the southern artic is annual (Fontaine, 1955; Østvedt, 1955; and others). Retardation of development in the large form may be sufficient to cause a much longer life cycle, perhaps biennial, which would not be competitively adaptive in the presence of the small form.

ACKNOWLEDGMENTS

I wish to express my sincere gratitude and appreciation to Dr I. A. McLaren, my research director, for making his collections available for investigation, and for his valuable advice concerning both the research and the manuscript. I am most grateful to Dr J. R. Shea, Jr. for his instruction and continuous encouragement during the cytophotometric analysis.

The financial support for this research was supplied through a grant to Dr I. A. McLaren from the National Research Council of Canada.

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A Laboratory Study of Particulate and Filter Feeding of the Northern Anchovy (*Engraulis mordax*)

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LEONG, RODERICK J. H., AND CHARLES P. O'CONNELL. 1969. *A laboratory study of particulate and filter feeding of the northern anchovy (Engraulis mordax).* J. Fish. Res. Bd. Canada 26: 557–582.

Observations of feeding behavior demonstrated that *Engraulis mordax* captures food by two distinctly different kinds of attack — biting and filtering. *Artemia* adults in high concentration evoke a biting attack and *Artemia* nauplii in high concentration evoke a filtering attack.

Feeding trials with *Artemia* adults produced the equation $w = 18.1\ T^{0.359}\ W^{1.138}$, where w is weight of food consumed in miiligrams, T is time in minutes, and W is fish weight in grams. Density had no effect over the range of 1–25 organisms per liter. Trials with adult *Artemia* also indicated that the maximum capacity of the digestive tract in milligrams is 93.3 W + 53.1.

Feeding trials with *Artemia* nauplii produced the equation $n = 6.31T^{0.970}W^{0.520}\ D^{0.594}$, where n equals the number of nauplii consumed. Density (D) had a noticeable effect over the range 292–1120 organisms per liter. The volume of water filtered per minute was determined on the basis of this equation.

The difference between the exponents for weight in the two kinds of feeding can be explained by the probability that when food is abundant filtering rate varies largely with area of mouth opening whereas particulate feeding rate varies largely with capacity.

From the filtering rates determined in this study and estimates of filter food concentration in the sea it is hypothesized that *E. mordax* cannot obtain its daily nutritional requirement by indiscriminate filtering alone.

Received September 25, 1968

INTRODUCTION

IVLEV (1961) commented that in trophic ecology first consideration must be given to questions of feeding intensity. Some knowledge of intensity or rate of feeding is necessary to develop hypotheses concerning the ability of fishes to obtain their nutritional requirements from various plankton regimes in the sea, but as Ivlev suggested, rate indices are more easily determined by experimental methods than from observations made in the natural environment. In this report the results of laboratory experiments on the particulate and filter-feeding rates of the northern anchovy, *Engraulis mordax*, a planktophage schooling fish of the northeastern Pacific, are described. Feeding is studied, within certain limits, in relation to fish size, food density, and food size. The adults of the brine shrimp, *Artemia salina*, were used as large food organisms to characterize particulate feeding and their nauplii were used as small food organisms to characterize filter feeding.

Hiatt (1951), who reviewed the literature on food and feeding habits of engraulid species, found that some were predominantly phytoplankton

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feeders and others predominantly zooplankton feeders. In his own study of the nehu, *Stolephorus purpureus*, based on stomach contents and plankton samples, he suggested that the lack of phytoplankton in the diet could be attributed to the fact that diatoms and dinoflagellates are scarce in Hawaiian waters. He showed, furthermore, that *S. purpureus* definitely preferred crustacean components of the zooplankton, and that in areas where large crustaceans were more available the fish were characteristically larger and appeared to select these organisms. The volume of food in the stomach was also generally higher in fish from the areas rich in large crustaceans.

The insight provided by the above kind of field information can undoubtedly be increased by laboratory-determined information on feeding rate. Knowledge of the diet of *E. mordax* from examination of stomach contents, though it suggests that the species utilizes both zooplankton and phytoplankton, is still too limited for a meaningful analysis. The feeding rates determined in this study should permit some evaluation of the food potential of plankton in nature. In this regard, the possibilities of achieving the daily nutritional requirement are discussed for one plankton situation in southern California waters.

FEEDING BEHAVIOR

Laboratory observations revealed that the anchovy feeds by "filtering" on high concentrations of nauplii of *Artemia salina* about 0.6 mm long, and by directed predatory snapping, or "biting," on *Artemia* adults 5–10 mm long. The occurrence of two methods of attack in relation to a difference in food suggested a priori that separate feeding rates should be calculated. Before the experimental results are presented, the two feeding behaviors will be described.

Some of the features that distinguish the two kinds of attack are summarized in Table 1 for two feeding trials in which food was presented in abundance at one end of a 30,000 gal tank with water 8 ft deep. Motion pictures were taken during the first few minutes of feeding and measurements were made on six fish in each picture sequence. The definitive difference is in duration of mouth opening. The average duration is more than 10 times greater in filtering than in biting, and the shortest filtering duration is more

TABLE 1. Distinguishing features of biting and filtering.

Type of activity	No. of fish observed	Mouth opening duration (*sec*)			Mouth opening rate (*no./5 sec*)	Turning rate (*no./5 sec*)
		Avg	Max	Min		
Biting on *Artemia* adults	6	0.15	0.25	0.09	9.4	9.7
Filtering on *Artemia* nauplii	6	1.72	4.45	0.63	2.9	1.3

than twice the longest biting duration. Another difference is the maximum rate of mouth opening, which is indicated by the average rates determined from the motion pictures. These are 9.4 openings in 5 sec for biting and 2.9 openings in 5 sec for filtering. Records of visual observations at other times indicate that mouth opening rate for filtering may sometimes be as high as one per second, but even this is distinctly lower than the biting rate.

The greater turning rate in feeding on adult *Artemia* indicates a "feeding frenzy," in which schooling is entirely abandoned. The introduction of abundant *Artemia* adults invariably induces a frenzy, but the intensity and duration vary greatly, probably in relation to such factors as tank size, number of fish, and state of hunger. The frenzy does not continue indefinitely in any feeding situation. In the instances above, it subsided noticeably after 5 min and by 10 min schooling was the dominant pattern, though food density was still high and considerable feeding was taking place.

Little if any frenzy occurs when *Artemia* nauplii are introduced. Though swimming speed may increase, schooling is usually maintained during filter feeding as long as a dozen or more fish are present. When fewer fish are present, they often move independently with occasional schooling.

The two kinds of feeding differ also in locomotion and directivity. In a typical bout of filtering the anchovy propels itself with five or six vigorous tailbeats while the mouth is agape. The mouth closes just before the last tailbeat, which is generally stronger than the others, and this is followed by a short glide. The glide is usually followed immediately by the next filtering bout, and a series of these bouts — as many as 60 a minute, although 30 is typical — forms a rhythmic pattern. When the mouth is agape the tailbeat amplitude increases, but lateral head movement decreases, so that the fish filters in a straight line. Figure 1 shows a few anchovies filter feeding on *Artemia* nauplii. It must be pointed out that this kind of gaping often occurs in the absence of food, sometimes shortly after a heavy feeding, suggesting that the activity may have functions other than feeding.

In the biting attack tailbeating usually stops as the mouth starts to open so that the fish captures the food particle while gliding. The duration of the glide may be no more than a few tenths of a second, but motion picture sequences suggest that the glide effectively eliminates, over the last few centimeters of approach to the food particle, the lateral head movement that occurs in ordinary swimming. Tailbeating in the biting attack does not differ from tailbeating in ordinary swimming at moderate speed. Though biting may occur at a high rate, it is not rhythmic, but probably depends on food contact. In general the biting attack is directed at individual organisms but the filtering attack is not. In the present study all presentations of *Artemia* adults elicited biting and all presentations of nauplii elicited filtering.

PARTICULATE FEEDING ON ADULT *ARTEMIA*

MATERIALS AND METHODS

Information on particulate feeding was obtained from a series of trials in which selected numbers of anchovies were allowed to feed for predetermined periods of time on measured quantities of adult *Artemia*.

Feeding trials were carried out in two tank arrangements (Fig. 2). The first tank used was a rectangular concrete structure 10.7 × 4.6 m with water at a depth of 1.25 m. It was divided into two large and one small middle compartment by two partitions of opaque plastic sheeting. Each partition included a vertically sliding gate near one end. One large compartment, with a capacity of 26 m^3 of water, was used as the experimental chamber and the other was used as a holding chamber. The small middle compartment served as a fish sorting and transfer chamber. With this arrangement and a few auxiliary movable screens, any desired number of fish could be segregated from a large school in the holding chamber and admitted to the experimental chamber without being removed from the water or immobilized.

The second tank was smaller but of similar design. It consisted of two circular, plastic swimming pools joined by a trough. The pools and the trough were separated by vertically sliding gates of fine mesh netting. Each pool was 3.05 m in diameter and held 3.65 m^3 of water at a depth of 0.5 m. In each arrangement, fresh, filtered sea water was delivered to the pool continuously except during trials when the flow was stopped to eliminate water movement in the pool and prevent loss of food organisms through the drain. Temperature for all trials, with *Artemia* adults or nauplii, ranged between 16 and 19 C.

In preparation for a series of trials, 200–400 anchovies, transported from commercial bait receivers in San Diego Bay, were placed in one of these tanks and allowed to move freely between the chambers. They were considered established and ready for feeding trials when mortalities had become negligible and the response to daily feeding of *Artemia* adults was strong. This required about 1 week.

Before each trial the entire school was confined to the holding chamber and deprived of food for at least 32 hr to insure that all fish would have empty alimentary tracts. Trial subjects were segregated into the transfer chamber and allowed to remain there undisturbed for 10 min or more before a trial.

The food situation was established by dispersing a known wet volume of *Artemia* as homogeneously as possible throughout the experimental chamber. The same wet volume, 450 cc, was used in all trials except those with six fish. This volume, estimated to contain 91,000 (±10,000) *Artemia* from 5 to 10 mm long and averaging 7 mm, produced a density of 3.5 organisms per liter in the large concrete tank and a density of 25 organisms per liter in the small circular tank. The wet volume was varied to obtain approximate densities of 1, 10, and 100 organisms per liter for the six-fish trials in the smaller tank. For all trials the *Artemia* were strained through $\frac{1}{16}$-inch mesh hardware cloth to eliminate smaller sizes before volumes were measured. No attempt was made to separate copulating pairs and for this reason actual food particle densities might have been somewhat lower than the estimated number of *Artemia* per unit volume.

Although food organisms were homogeneously distributed at the start of trials, visible unevenness developed during the course of some trials. Ivlev (1961) indicated that the feeding rate may vary with degree of patchiness, at least for some fishes. The influence of this factor is not known for the present experiment because we do not have measurements of distributional change. However, the observed differences in distribution did not appear to restrict the movements or feeding activity of the fish.

Once the food situation was established and the waiting period completed, the fish were allowed to enter the experimental chamber and feed for the predetermined time period. Closing of the gate immediately after admission initiated the time period, and introduction of a hinged crowder for capture terminated it. In all tests the fish to be examined were pithed within 2 min after introduction of the crowder, immediately measured, and weighed, then placed in formalin with the body cavity opened.

The distribution of trials in respect to five categories of school size, five categories of food density, and eight categories of feeding duration is shown in Table 2. All fish were killed from the 1-fish and 6-fish trials, 2–4 from the 4-fish trials, and 10–13 from the 16- and 64-fish trials. The trials listed in the table represent 24 of a possible 200 combinations of the arbitrarily chosen categories. The irregularities in the arrays of all three variables are due to the exploratory nature of the study.

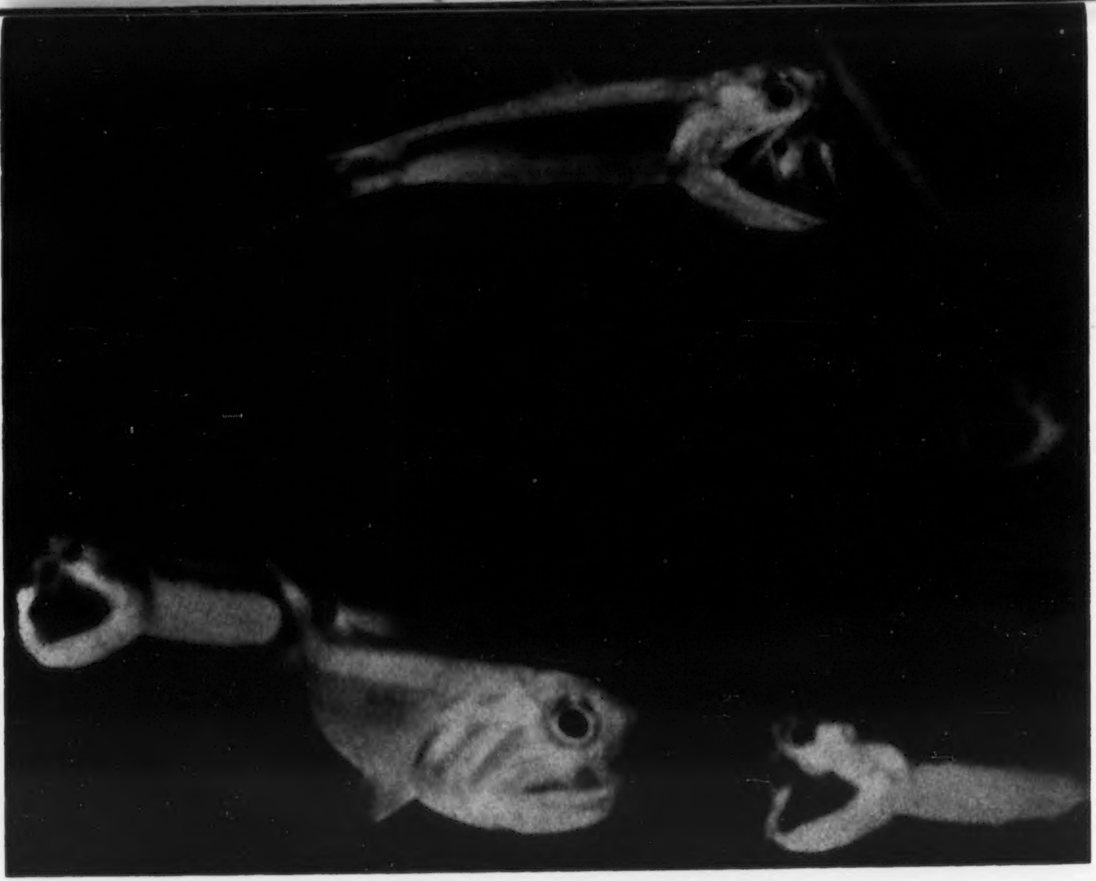

FIG. 1. Anchovies filter feeding on *Artemia* nauplii.

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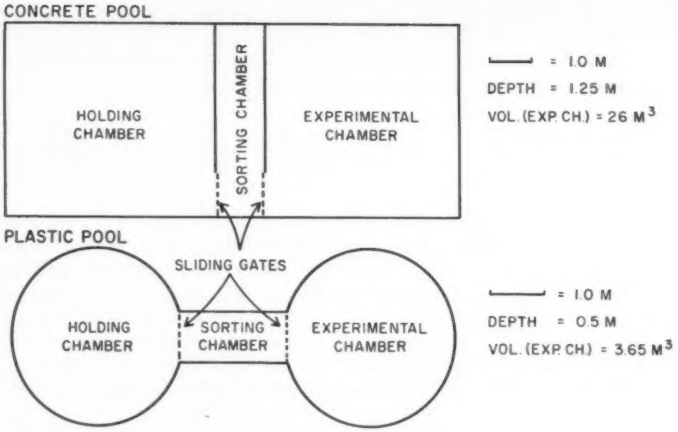
CONCRETE POOL
HOLDING CHAMBER
SORTING CHAMBER
EXPERIMENTAL CHAMBER
= 1.0 M
DEPTH = 1.25 M
VOL. (EXP. CH.) = 26 M³
PLASTIC POOL
SLIDING GATES
HOLDING CHAMBER
SORTING CHAMBER
EXPERIMENTAL CHAMBER
= 1.0 M
DEPTH = 0.5 M
VOL. (EXP. CH.) = 3.65 M³

FIG. 2. Diagrams of experimental pools used for feeding experiments.

A total of 291 anchovies from 77 feeding trials were examined. The average standard length of all specimens used in the analysis was 79.4 mm (range, 65–122 mm) and the average weight was 5.14 g (range, 2.7–18.5 g). Although length–weight information was useful for evaluating the effect of size on feeding it should be noted that size variability between trials was not homogeneous.

Two procedures were used in estimating the weight of *Artemia* consumed by individual anchovies. Organisms in the pharynx, oesophagus, and stomach were pooled and weighed. Organisms in the intestine were not weighed because they were in various stages of digestion. Instead, they were counted and converted to wet weight with a factor of 2.05 mg per *Artemia*. This was the average wet weight of 2000 *Artemia* taken from the stomachs and oesophagus of several formalin-preserved fish; the weight of these *Artemia* was undoubtedly less than that of unpreserved organisms due to dehydration and leaching.

TABLE 2. Number of trials for different combinations of school size, food density, and feeding time.

	School size and (in parentheses) no. of adult *Artemia* per liter									
	1		4		6			16		64
Feeding time (*mm*)	(3.5)	(25)	(3.5)	(25)	(1)	(10)	(100)	(3.5)	(25)	(3.5)
3.75	–	–	–	–	–	–	–	–	–	1
5.00	–	–	–	–	3	4	3	–	–	–
7.50	–	10	–	3	–	–	–	–	1	1
15.00	10	–	3	–	–	–	–	1	1	1
30.00	–	10	3	–	–	–	–	1	1	1
60.00	–	10	3	–	–	–	–	–	1	1
120.00	–	–	–	–	–	–	–	3	–	–
240.00	–	–	–	–	–	–	–	1	–	–

Although a few trials were carried out at 120- and 240-min feeding duration, the relation between food density and amount of food eaten was based only on trials of 60 min duration or less. The average weight of food in the intestine relative to weight of food in the entire alimentary tract increased with the length of the feeding period as follows:

Min of feeding	3.75	7.50	15.0	30.0	60.0
% of food in intestine	0	1.2	3.7	5.6	12.4

Virtually all fish had full intestines after 60 min, whereas only about one-quarter of the fish reached that state feeding for 30 min. If it is assumed that the rate of movement through the intestine is constant and that one intestine measure is eliminated every half hour, the loss after 60 min would be 5.6% of the quantity consumed in the first 30 min. Since such a loss is relatively small, the amount in the alimentary tract after 60 min is considered an acceptable though slightly conservative representation of the food consumed during the period. For longer periods, loss through defecation must be assumed to be unacceptably high. The data from these longer periods, however, proved useful in inferring the maximum capacity of the anchovy alimentary tract.

Relation of Food Consumed to Four Variables

Multiple regression appeared to be suitable for analysing the data. Preliminary graphic analysis showed that the variables were associated and that logarithmic transformation rectified curvilinear relationships to linear form; the regression model adopted was

$$w = \mathrm{K} + a \,\mathrm{Log}\, \mathrm{T} + b \,\mathrm{Log}\, \mathrm{W} + c \,\mathrm{Log}\, \mathrm{D}$$

where w = weight of *Artemia* consumed in milligrams; K = regression constant; T = feeding duration in minutes; W = weight of fish in grams; D = food density in number of *Artemia* per liter of water; and a, b, and c = the respective coefficients to be estimated.

The regression analysis was applied first to the five school size categories, and then to all categories pooled, with density deleted as a variable. Table 3 shows the estimated regression coefficients and standard errors, ranges of the variables, and the number of trials for each of these arrays. Because variation within trials was large, coefficients were computed for trial variates rather than for individual fish. Thus, feeding duration and food density are set values, but fish weight and food consumed per fish are averages for the fish sampled from each trial. The one-fish trials are exceptions by definition.

Table 3 does not indicate significant differences among the school groups for the coefficients a, b, or c, indicating that school size did not have a major effect on feeding. The coefficients a, for the effect of feeding time, are all significantly higher than zero and lower than unity (all statements of statistical significance are based on probability level of 0.05). The coefficients b, for the effect of fish weight, do not differ significantly from unity, and all but the value for the 64-fish category differ significantly from zero. The low coefficient and large standard error for the 64-fish group reflects the narrow range in fish weights rather than any real inconsistency with the other groups.

TABLE 3. Estimated coefficients by school size for feeding on *Artemia* adults.

	School size and (in parentheses) no. of trials					
Coefficients	1 (40)	4 (12)	6 (10)	16 (6)	64 (5)	Pooled[a] –
Est. *a*	0.473	0.411	–	0.361	0.352	0.359
σa	0.065	0.065	–	0.118	0.067	0.031
Range of T	7.5–60.0	7.5–60.0	5.0	7.5–60.0	3.75–60.0	3.75–60.0
Est. *b*	1.038	0.754	1.010	1.224	0.221	1.138
σb	0.227	0.207	0.362	0.268	0.806	0.096
Range of W	2.6–7.0	3.0–6.3	4.1–6.1	3.8–11.1	3.6–4.5	2.6–11.1
Est. *c*	–0.130	0.102	–0.073	–0.079	–	–
σc	0.060	0.076	0.023	0.134	–	–
Range of D	3.5–25.0	3.5–25.0	1.0–100	3.5–25.0	3.5	–
Est. *k*	1.301	1.361	1.696	1.275	1.796	1.257
σk	0.143	0.085	0.248	0.154	0.519	0.076

[a] The method of pooling is explained in the text.

Of the coefficients *c*, for density, only the negative value for the 6-fish, school-size category differs significantly from zero, implying that the rate of food intake decreased with density for this group. The 6-fish trials spanned a much wider range of density than the other school size-groups, however, and the data from these trials suggest that the highest density (100 *Artemia* per liter) may have suppressed feeding.

The coefficients for the pooled array are based not on trial variates, but rather on variates for each of the cells in Table 2. Here again feeding duration and food density are set values, but fish weight and food consumed per fish are averages for all fish sampled from a given cell. In this way each cell representing a different combination of school size, feeding duration, and food density tested is given equal weight in the final regression. Table 4 shows the number of fish examined, the values for the three variables, and the amount of food consumed per fish for each of the combinations. The two combinations with feeding periods greater than 1 hr were excluded from the regression analysis for reasons explained in the previous section and are not shown in the table. The combination with density of 100 *Artemia* adults per liter is also excluded from the final regression, in which case it can be said that densities between 1- and 25-*Artemia* per liter have no demonstrable effect on the amount of food consumed. The last two columns in the table show expected amount consumed, as estimated from the final regression, and the percentage deviation of the actual amount consumed from the expected amount. The deviations give an impression of how representative the regression is for the data.

TABLE 4. Array of variates for pooled multiple regression.

School size	No. of fish examined	Feeding duration (*min*)	Wt (*g*)	Food density (*Artemia/ liter*)	Amount consumed (*mg*)	Expected amount consumed (*mg*)	Deviation (%)
1	10	7.50	3.80	25.0	138.5	170.2	−23
1	10	15.00	3.63	3.5	241.7	207.2	+14
1	10	30.00	4.93	25.0	387.9	376.7	+3
1	10	60.00	4.07	25.0	386.8	388.5	0
4	10	7.50	5.52	25.0	264.2	260.4	+1
4	10	15.00	3.44	3.5	200.2	195.0	+3
4	10	30.00	4.56	3.5	331.9	344.7	−4
4	10	60.00	4.71	3.5	460.3	458.8	0
6	15	5.00	4.78	1.0	235.8	191.0	+19
6	24	5.00	5.23	10.0	235.3	211.7	+10
16	10	7.50	5.01	25.0	212.4	233.2	−10
16	10	15.00	4.22	3.5	252.6	246.0	+3
16	14	15.00	9.61	25.0	626.7	627.9	0
16	9	30.00	3.76	3.5	337.0	276.7	+18
16	13	30.00	11.08	25.0	964.2	947.1	+2
16	10	60.00	4.38	3.5	418.4	422.4	−1
64	10	3.75	4.50	3.5	154.6	160.9	−4
64	10	7.50	4.21	3.5	147.9	191.3	−29
64	10	15.00	3.58	3.5	224.3	204.0	+9
64	10	30.00	4.43	3.5	285.9	333.5	−17
64	10	60.00	4.20	3.5	373.4	402.7	−8

The regression coefficients and the constant for the pooled data are our best estimates and are taken to be a satisfactory representation of all of the school-size categories. Density was eliminated as a variable from the final calculation because its coefficient, *c*, was not significantly different from zero. The validity of the other coefficients is illustrated by Fig. 3. In Fig. 3A the average amount consumed is plotted against feeding time for each school-time-density combination shown in Table 4. Average fish weights are indicated, and the points are connected by rank in fish weight. The tendency for these lines, whose slopes are graphic approximations of the coefficient *a* for fish of similar weight, to parallel the line based on the regression, indicates that the latter is a satisfactory fit, and that the estimated *a* shows the effect of time on feeding independent of fish weight. In Fig. 3B the average amount consumed is plotted against the average fish weight; feeding times are indicated and the points are connected by equal time periods. Again the lines tend to parallel the line based on the calculated regression, indicating that the coefficient *b* in the latter represents the effect of fish weight on feeding independent of feeding time. The fact that the 5-min values are at a higher level than the 7.5-min values is attributed to experimental error.

The percentage deviations of actual from expected amounts consumed, shown in the last column of Table 4, suggest some slight differences in the

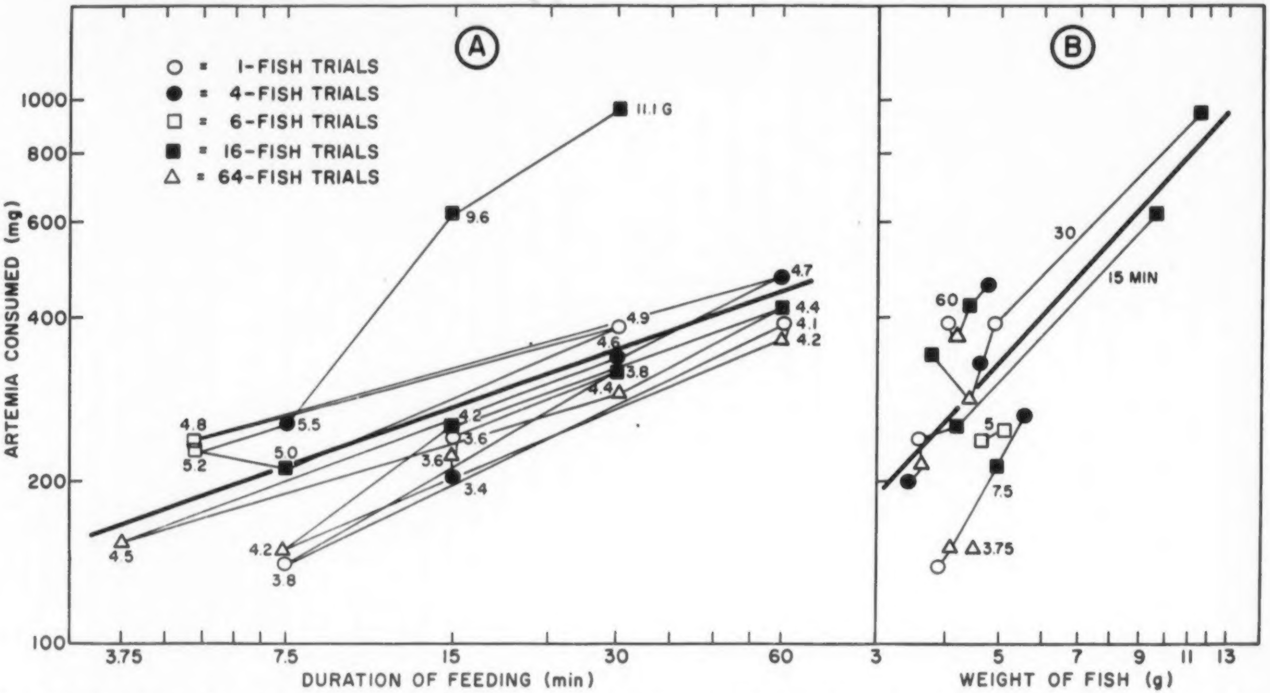

FIG. 3. The relation of feeding on *Artemia* adults to two variables. (A) Milligrams of *Artemia* adults consumed in relation to feeding time. Fish weight is noted for each point. (B) Milligrams of *Artemia* adults consumed in relation to fish weight. Feeding time is noted for each connected series of points. The thick lines are based on the calculated regression. See text for further explanation.

results for different school-size categories. Whereas positive and negative values are approximately equal for the 1-, 4-, 6-, and 16-fish categories, most of the values for the 64-fish group are negative, suggesting, perhaps, that the 64-fish group may have been feeding at a slightly lower rate than the others under the conditions of this experiment. In terms of actual results, the model appears to be representative for the pooled array. The greatest positive deviation is 19%, the greatest negative deviation 29%, and the average deviation 8.5%.

The coefficients for the pooled array appear in equation form as:

$$\text{Log } w = 1.257 + 0.359 \text{ Log T} + 1.138 \text{ Log W} \qquad (1)$$

or

$$w = 18.1 \text{ T}^{0.359} \text{ W}^{1.138} \qquad (2).$$

Equation 2 gives the weight of *Artemia* adults that an anchovy of weight W can be expected to consume after T minutes of feeding on densities between 1 and 25 *Artemia* per liter. This equation is only applicable in a strict sense to feeding periods up to 60 min, and to fish weighing between 3.6 and 11.3 g.

Differentiation of equation 2 with respect to time gives

$$dw/d\text{T} = 6.49 \text{ T}^{-0.641} \text{ W}^{1.138} \qquad (3).$$

From this equation it is possible to estimate the rate, e.g., weight of *Artemia* being consumed per minute, for fish weighing W grams after T minutes of feeding. It is obvious from equation 3 that rate decreases with time.

Although these equations are only valid for feeding periods up to 60 min it is likely that the anchovy will continue to feed beyond this point and eventually reach but not exceed some particular level of fullness. Where food is in surplus, such a level can be considered the maximum capacity of the alimentary tract. The average weight of *Artemia* consumed per gram of fish in each time period up to and including 240 min are:

Min of feeding	3.75	5.0	7.5	15	30	60	120	240
Mg *Artemia* per g fish	34.4	43.0	41.1	63.1	80.2	94.4	104.5	107.6
No. of fish	10	57	40	54	52	40	29	9

Food consumed per gram of fish is maximal at 240 min, but the difference between 120- and 240-min categories is negligible. Under these circumstances the fish from the 120- and 240-min trials should demonstrate the relation between maximum capacity and fish weight. Figure 4 shows the relationship for all individuals from these long period trials. The line describing the relation,

$$w_{\max} = 53.1 + 93.3 \text{ W} \qquad (4)$$

expresses the average maximum capacity for fish weighing W grams.

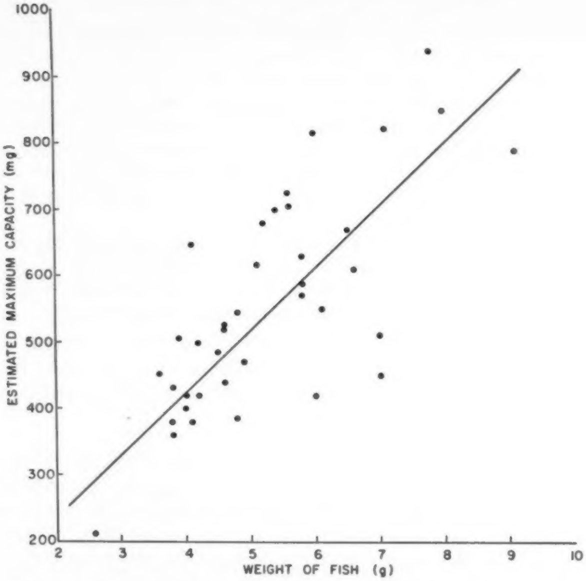

FIG. 4. Relation between estimated maximum capacity and weight of fish. Each point represents a fish that has fed for 120 or 240 min. Milligrams consumed are for formalin-preserved *Artemia* adults.

FILTER FEEDING ON *ARTEMIA* NAUPLII

MATERIALS AND METHODS

Information on filter feeding was obtained from a series of trials in which selected numbers of anchovies were allowed to feed for predetermined time periods on high concentrations of *Artemia* nauplii. The number of nauplii consumed was estimated from alimentary tract contents.

All trials with *Artemia* nauplii were carried out in the previously described circular pools with interconnecting trough. The period of food deprivation and the methods of introducing, retrieving, and processing fish for storage in formalin were the same as in the previous experiment. The major differences, aside from the size of the food organism used, were in the assessment of the food concentration and in the measurement of alimentary tract contents.

The food situation was established by dispersing large quantities of newly hatched nauplii, about 0.6 mm long, in the tank. Ten g of *Artemia* eggs (San Francisco) were incubated for each trial, except for the 6-fish trials, in which quantities were varied. Immediately after dispersing the nauplii and before admitting fish, 10 24-cc water samples were taken at regular intervals around the pool for estimation of density of nauplii. Another set of 10 samples was taken at the end of the trial after the fish were removed and the tank restirred. The average of the two sets was used as the index of density and the coefficient of variation was about 10% for a set of 10 samples. In the trial with the largest number of fish (64) and the longest feeding period (60 min), the post-trial estimate was only slightly more than half the pre-trial estimate. In trials with fewer fish and shorter feeding periods the differences were much less.

A series of samples, taken without fish in the pool, demonstrated that some degree of patchiness may develop during longer trials. No adjustment was possible, however, because we had neither measurements of such distributional change nor knowledge of its actual effect on filter feeding.

The number of nauplii consumed by each fish was estimated from volumetric aliquots of alimentary tract contents. All nauplii from the pharynx, oesophagus, and stomach were washed into a large beaker to which water was added to raise the volume to 2000 cc. Ten samples, each 10 c in volume, were removed from the beaker for enumeration. These sets generally had a standard error which was about 3% of the mean. The number of nauplii in the intestine was estimated separately. The same procedure was used except that the beaker volume was raised only to 1000 cc although the sample volume remained at 10 cc. When an intestine appeared to contain fewer than 500 nauplii, a total count was made. Addition of the two estimates produced an estimate of the total number of nauplii in the fish.

These values should be reasonable estimates of the total amounts ingested by the fish, although some uncertainty attaches to the 30- and 60-min feeding periods. All fish feeding for 60 min had material along the entire length of the intestine, whereas only about one-quarter of those feeding for 30 min showed this condition. The relative abundance of nauplii in the intestine for different feeding periods is:

Min of feeding	7.5	15	30	60
% nauplii in intestine	19.6	19.0	17.4	16.1

If the rate of movement through the intestine is approximately constant, it may be inferred that the amount lost by defecation after 60 min would be the quantity in the intestine at 30 min. Since the ingestion rate is virtually constant, as is shown later, it follows that the percentage lost after 60 min would be approximately half the 30-min value, or 8.7%. We do not consider this loss excessive and will therefore include the 60-min trials in the study of filter-feeding rate.

The distribution of trials in relation to five categories of school size and five categories of feeding duration is shown in Table 5. All fish were sampled from the 1- and 6-fish trials, 2–4 fish from the 4-fish trials, 5–13 fish from the 16-fish trials, and 10 fish from the 64-fish trials. A total of 210 anchovies from 75 feeding trials was examined.

TABLE 5. Number of trials for different combinations of school size and feeding time.

Feeding time (*min*)	School size				
	1	4	6	16	64
5.0	–	–	11	–	–
7.5	10	3	–	2	2
15.0	10	3	–	2	1
30.0	10	3	–	2	1
60.0	10	3	–	1	1

As in the preceding experiment, it was impractical to control fish size, so trials are not homogeneous in this respect. Average trial weights, however, yielded a satisfactory description of the effect of this factor on amount eaten. Average standard length of all specimens for which alimentary tract contents were estimated was 73.3 mm (range, 5.6–11.9 mm) and the average weight was 3.64 g (range, 1.0–17.9 g).

The array of trials is not categorized in respect to density because this factor was not rigidly controlled during most of the experiments. Although the abundance of *Artemia* eggs was standardized at one weight for practically all trials, variations in hatching success caused a considerable range of densities within each school-size category. This information was sufficient to characterize the effect of density on feeding, at least for the limited range of densities investigated.

The analysis of feeding on nauplii was carried out on the basis of numbers consumed rather than weight consumed because these very small organisms had to be washed out of inaccessible parts of the alimentary tract and it would have been difficult to reconstitute them as a wet-weight mass. Nauplii from a few fish were weighed and then counted to produce a weight conversion factor so that results with nauplii could be compared to results with adult *Artemia*. The average nauplius weight obtained in this way was 0.011 mg. This factor is relevant only for nauplii from the alimentary tracts of fish stored in formalin and is probably less than the weight of unpreserved nauplii.

RELATION OF FOOD CONSUMED TO FOUR VARIABLES

The analysis of feeding on nauplii is similar to that for feeding on *Artemia* adults, but is more complicated because of greater variation, some anomalous trials, and the importance of density as a factor. As in the preceding experiment, the multiple regression analysis appeared to be a suitable method for examining the data, so the regression model adopted is again of the general form

$$\text{Log } n = \text{K} + a \text{ Log T} + b \text{ Log W} + c \text{ Log D}$$

where n = number of nauplii consumed; K = regression constant; T = feeding duration in minutes; W = weight of fish in grams; D = food density in nauplii per liter; and a, b, and c = the respective coefficients to be estimated.

The regression analysis was applied to each of the school-group categories separately and then to the 16-and 64-fish categories pooled. Table 6 shows the number of trials, the estimated coefficients and standard errors, and the ranges of the variables for each of these groupings. The equation based on the pooled 16- and 64-fish categories was selected as the best general description

TABLE 6. Estimated coefficients by school size for feeding on *Artemia* nauplii.

	School size and (in parentheses) no. of trials					
Coefficients	1 (40)	4 (12)	6 (11)	16 (7)	64 (5)	16 and 64 pooled[a]
Est. a	1.014	1.620	–	1.121	0.910	0.970
σa	0.141	0.246	–	0.088	0.088	0.058
Range of T	7.5–60.0	7.5–60.0	5.0	7.5–60.0	7.5–60.0	7.5–60.0
Est. b	1.439	2.092	–1.377	0.438	0.692	0.520
σb	0.555	0.797	0.758	0.069	0.745	0.069
Range of W	2.1–5.4	1.3–4.5	1.5–2.8	2.4–12.3	2.6–3.3	2.4–12.3
Est. c	0.222	0.294	0.798	0.951	0.485	0.594
σc	0.314	0.712	0.207	0.210	0.151	0.118
Range of D	321–950	254–617	82–707	354–854	292–1120	292–1120
Est. k	–0.397	–2.830	1.164	–2.636	1.074	0.800
σk	1.229	4.274	1.447	1.044	0.612	0.362

[a] The manner of pooling is explained in the text.

of the feeding response. The results for these two largest school-size categories appeared to be consistent with each other, whereas results for the three smaller school-size categories were each deficient in some respect. The nature and probable causes of these deficiencies will be examined before the results of the analysis for the two larger school groups are discussed.

One inconsistency in the results for different school sizes is reflected by the coefficients for the effect of nauplii density on food consumption (*c* in Table 6). The coefficients shift from low values with wide variation for the 1- and 4-fish groups to higher values with relatively low variation for the 6-, 16-, and 64-fish groups. The values for the latter three groups are significantly higher than zero, showing that nauplii density had a real effect on amount consumed. Graphic analysis likewise showed a noticeable relation between feeding and density for the three larger groups but not for the two smaller groups. The presence of this relation for the larger groups and its absence for the smaller groups suggests that school size itself did affect the estimation of *c*. The lower variation with larger school groups may be due in part to the fact that more fish were sampled per trial, but broader and more consistent pool coverage by individuals when feeding in larger schools may also have been a factor.

Where nauplii are present in even moderate abundance the anchovy tends to filter by rhythmic gaping bouts. In the 16- and 64-fish trials the fish invariably schooled well and circuited the tank regularly, whereas in the 4- and 6-fish trials schooling was transient and circuiting variable. Individuals in the 1-fish trials sometimes circuited the pool and sometimes filtered in restricted areas. Since nauplii were not always distributed homogeneously in the pool, noncircuiting individuals could easily have experienced concentrations different from those estimatd from the water samples. The more uniform tank coverage by individuals in the larger groups, on the other hand, presumably enabled them to experience an average concentration close to that indicated by the water samples. On the basis of these findings we judge that the 1- and 4-fish groups were not large enough to respond fully or consistently to the present experimental situation, and they will be eliminated from the analysis.

Although the results from the 6-fish trials for the effect of density of nauplii on amount consumed (*c* in Table 6) are not inconsistent with the results from the two larger school-size categories, the coefficient for the effect of fish weight on amount consumed (*b*) is very much different, at −1.38, from those obtained for the other groups; a negative relation is unreasonable because it indicates that smaller fish filter at a greater rate than larger fish. Its occurrence may be due to the brevity of the feeding period — 5 min — for all of the 6-fish trials. A possible explanation is that the smaller fish began feeding sooner than the larger fish after entry into the experimental pool. With only a short feeding period and a size-related delay in start of feeding, a negative relation between fish size and amount consumed is possible. In view of this the 6-fish trials are eliminated from the final regression.

It can be seen from Table 6 that the estimated coefficients for the 16- and 64-fish categories are not significantly different. If the differences between these two coefficients are significant the samples were insufficient to show it. The samples were adequate to demonstrate that the coefficients *a* and *c* were significantly higher than zero for both groups. The coefficient *b* was significantly higher than zero for the 16-fish group, but not for the 64-fish group, which had a very narrow range of weights. The results suggest that differences between the 16- and 64-fish groups that may be attributable to school size itself are small in relation to variation attributable to the other factors tested. With the reservation that small discrepancies do exist, the trials from the 16- and 64-fish categories are pooled to obtain a general filter-feeding model.

Table 7 shows the number of fish examined, the values for the three variables, and the amount of nauplii consumed per fish for the 16- and 64-fish trials. The values for fish weight and amount consumed are averages for the trial. How well the coefficients represent the trial data can be judged from Fig. 5. Figure 5A shows the relation between the quantity of food consumed and the period of feeding. Each point represents a trial (with fish weight indicated) and the points are connected by their rank in weight. The slopes of these lines may be considered as estimates of *a* independent of weight, but not of density. These lines are reasonably parallel with the line based on the regression, indicating a satisfactory fit.

TABLE 7. Array of variates for 16- and 64-fish trials with *Artemia* nauplii.[a]

School size	No. of fish examined	Feeding duration (*min*)	Wt (*g*)	Density (*nauplii/liter*)	Amount consumed (*no.*)	Expected amount consumed (*no.*)	Deviation (%)
16	5	7.5	4.06	641	4477	4293	+ 4
16	5	7.5	2.38	673	3305	3347	− 1
16	10	15.0	2.84	513	6520	6115	+ 7
16	13	15.0	12.31	854	18876	17752	+ 6
16	13	30.0	10.62	354	16693	19074	−12
16	10	30.0	2.95	435	10525	11074	− 5
16	10	60.0	3.98	402	29574	24180	+22
64	9	7.5	3.27	400	3197	2898	+10
64	10	7.5	2.86	1120	4777	4985	− 4
64	10	15.0	3.05	563	5801	6707	−14
64	10	30.0	2.56	292	7878	8116	− 3
64	10	60.0	3.04	437	20968	22087	− 5

[a] The expected quantity consumed was calculated from the final regression for these two school size groups.

On the assumption that feeding rate is constant, the number of nauplii consumed per minute in each trial has been plotted against average fish weight (Fig. 5B) and against density of nauplii present (Fig. 5C). In Fig. 5B the nauplii

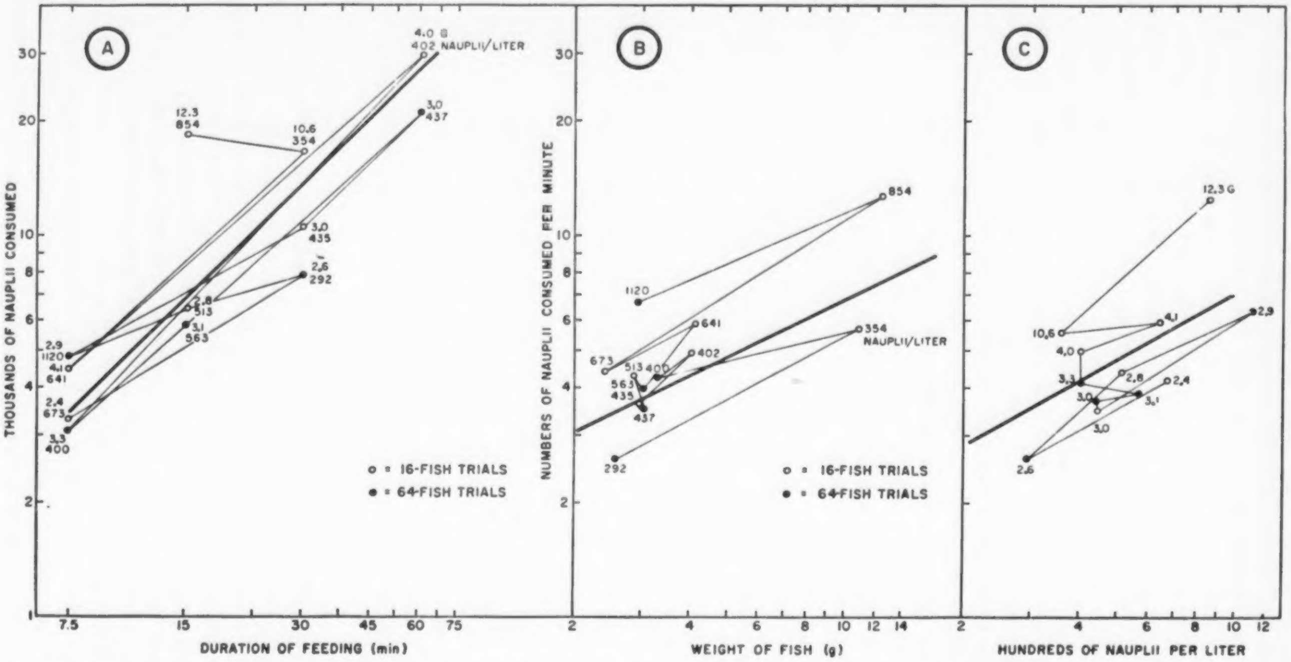

FIG. 5. The relation of feeding on *Artemia* nauplii to three variables. (A) The number of *Artemia* nauplii consumed in relation to feeding time. Fish weight (*upper number*) and food density (*lower number*) are noted for each point. (B) The number of *Artemia* nauplii consumed per minute in relation to fish weight. Density is noted for each point. (C) The number of *Artemia* nauplii consumed per minute in relation to density. Fish weight is noted for each point. The thick lines are based on the calculated regression. See text for further explanation.

density is given for each point, and the points are connected in consecutive order of density by straight lines. These lines, on the whole, parallel the heavy line whose slope represents the coefficient *b* in the final regression. It therefore appears that the calculated coefficient is representative of the effect of fish weight on feeding, independent of food density and time. In Fig. 5C, the mean fish weight is given for each trial point, and points have been connected in consecutive order of weight by straight lines. These lines also are reasonably parallel to the line representing the regression, and the calculated coefficient appears to be representative of the effect of density on feeding independent of fish weight and time.

The percentage deviations of actual from expected amount consumed, given in the last column of Table 7, is a further indication of the efficacy of the coefficients calculated for the two groups pooled. Only 3 of the 12 deviations are greater than 10%. Although most of the deviations for the 64-fish group are negative, none are large.

The coefficients for the 16- and 64-fish categories pooled (Table 6) appear in equation form as

$$\text{Log } n = 0.800 + 0.970 \text{ Log T} + 0.520 \text{ Log W} + 0.594 \text{ Log D} \tag{5}$$

or

$$n = 6.31 \ \text{T}^{0.970} \ \text{W}^{0.520} \ \text{D}^{0.594} \tag{6}$$

which gives the expected number of nauplii eaten after T minutes of feeding by fish weighing W grams on D nauplii per liter. This statement must be qualified to fit the conditions of the experiment, i.e., it is valid only for fish weighing 2.38–12.31 g feeding for periods not greater than 1 hr on densities ranging between 292 and 1120 nauplii per liter. Beyond these limits different relationships may apply. The length of the feeding period must be considered in relation to nauplii concentration, since fish may reach satiation in less than 1 hr on very high concentrations and reduce the rate of intake. The 60-min trials for the 16- and 64-fish groups do show, however, that the fish filter feed at uniform rate for at least 1 hr on a concentration of 400 nauplii per liter.

Equation 6 can be differentiated with respect to T to yield

$$dn/d\text{T} = 6.11 \ \text{T}^{-0.030} \ \text{W}^{0.520} \ \text{D}^{0.594} \tag{7}$$

which indicates the expected number of nauplii a fish will be consuming per minute after T minutes of feeding. The negligible exponent for T shows that feeding rate changes little within 1 hr.

With the assumption that the gill-raker apparatus retains *Artemia* nauplii with 100% efficiency, the rate of water filtration can be obtained by multiplying equation 7 by the reciprocal of nauplii density. Since density was defined as the number of nauplii per liter, it follows that the reciprocal, 1/D, would represent the volume of water containing one nauplius. The result of the multiplication is

$$dL/dT = 6.11\ T^{-0.030}\ W^{0.520}\ D^{-0.406} \qquad (8).$$

The negative coefficient for D implies that the anchovy water filtration rate is higher at lower densities. Solving equation 8 for the lowest trial density in the pooled series would therefore yield maximum filtering rates for the data upon which the equation is based. These would have to be regarded as conservative estimates of absolute maximum rates in that equation 8 may be valid for lower densities, but it is probable that the ultimate limits, dictated by mouth size and the proportion of time it can be kept open, would not be far beyond such estimates.

If D is set at 292 nauplii per liter, the minimum used in this series, and T is set at 1 min, the maximum filtering rate can be estimated for fish of different weights. For selected weights the estimated maximum rates would be, on the average:

Wt (g)	1	2	3	4	5	6	7	8	9	10	11	12
Liters/min	0.63	0.90	1.12	1.30	1.46	1.60	1.73	1.86	1.98	2.09	2.19	2.30

COMPARISON OF PARTICULATE AND FILTER FEEDING

Laboratory observations have shown that the anchovy procures food by filtration or directed predatory biting, depending on the size of the organisms. Experiments have shown that the quantities consumed and rates of consumption are functions of the duration of feeding, the size of the fish, and the density of the food. Comparison of the two kinds of feeding (Fig. 6) for a fish of one size, 4 g, shows that the effects of these factors are very different for each. Rates and quantities, plotted by weight for both modes of feeding, were computed from the equations developed in the preceding sections, with density of nauplii assumed to be 400 per liter. Numbers of nauplii consumed were converted to weight by the factor 0.011 mg per nauplius, determined earlier. Densities are comparable for the two kinds of organisms in that the equation for feeding on *Artemia* adults is applicable over the range 1–25 organisms, and the wet weight of 400 nauplii (4.4 mg) is equivalent to approximately two adults on the basis of the conversion factors derived in this study. The indicated level of maximum capacity (426 mg) is based on the relationship between maximum capacity and fish weight developed from the data for feeding on *Artemia* adults.

Comparison of the two rate curves during early feeding indicates that food is obtained much more rapidly by biting than by filtering. The rate curve for feeding on adult *Artemia* indicates that the biting rate is highest at the start of feeding but diminishes long before satiation is reached. The rate curve for filter feeding, by contrast, suggests that filtering is relatively uni-

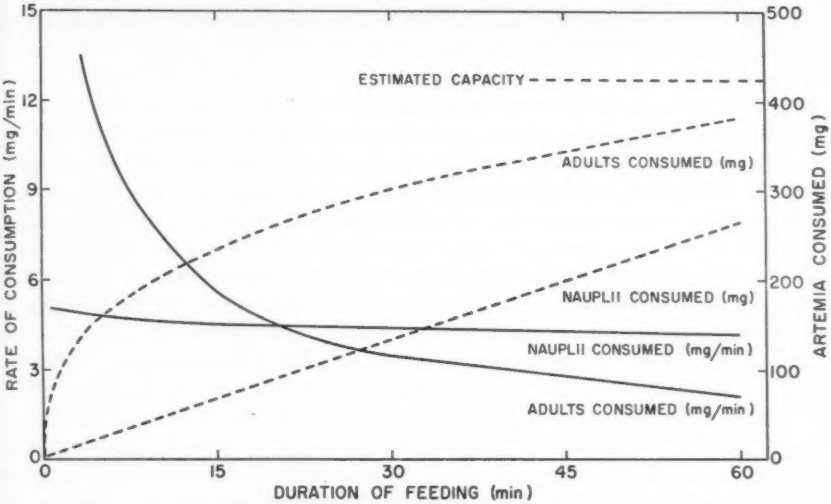

FIG. 6. Comparison of particulate and filter feeding rates for a 4-g anchovy. Particulate feeding curves are appropriate for concentrations of 2–50 mg of *Artemia* adults per liter. Filter feeding curves are appropriate for a concentration of 4.4 mg of *Artemia* nauplii per liter. The estimated maximum capacity for a 4-g anchovy is indicated as a horizontal line.

form during 1 hr and that the filtering rate is limited from the outset by the straining capacity of the fish. The biting rate indicated for 3.75 min of feeding means that a fish would be consuming 6 or 7 *Artemia* adults per min at that time, but the curve for amount consumed shows that over 140 mg, or about 70 *Artemia*, would already have been captured. This means that a 4-g fish should average at least 18 *Artemia* per min in the first few minutes, and judging from the motion pictures of initial activity, the rate could be considerably higher during the first minute.

But then why the decline in rate when the fish is so far short of maximum capacity? Feeding on abundant adult *Artemia*, it may be recalled, is accompanied by a "feeding frenzy" during the first quarter hour or so of feeding. The frenzy and its decline accord with the rapid decline in the rate of intake in the early minutes of feeding, but the reason for such a diminution in activity is not readily explainable. It is certainly a behavioral reaction to this kind of a food situation, and possibly its intensity and duration are governed by energy already expended and the degree of fullness achieved. After the frenzy the fish continue to accumulate food towards full capacity at a low rate. Thus, the fish will strive for full capacity, but it appears that obtaining some sizable fraction of it in a short time is of paramount importance, and it may be surmised that the feeding frenzy with its initial high rate of intake is an effective adaptation for taking quick advantage of small or infrequently encountered aggregations of large organisms.

The above discussion was concerned with fish of one weight, but the equations developed earlier show that feeding is also affected by weight, and differently for each kind of attack. Particulate feeding on adult *Artemia* varies as $W^{1.138}$ and filter feeding on nauplii varies as $W^{0.520}$. Though weight may not affect feeding directly, the exponents must reflect factors related to weight that do affect it, such as area of mouth opening, swimming speed, and food capacity. Examination of the probable relationship between these factors and weight offers some explanation of the difference between the two weight exponents.

In filter feeding, the nature of the activity suggests that rate should depend partly on the area of the mouth opening and partly on the swimming speed while the mouth is agape. Mouth opening would determine the cross-sectional area and swimming speed the length of the water column filtered. Isaacs (1965) offered several a priori models to explain growth rates of larval fish under different assumptions of feeding conditions. The statements of feeding rate (dQ/dt) associated with these models can also be applied to grown fish. For all models Isaacs assumed that weight of the fish (W) is proportional to length cubed (L^3), that mouth area is proportional to length squared (L^2), and that swimming velocity is proportional to the cube root of length ($L^{1/3}$). For the model most suitable to the present discussion, he suggested that if the water contains uniformly fine particles and the fish feed by swimming at a constant power-to-weight output and capture a fixed proportion of the particles in a column of water whose cross-sectional area is proportional to the mouth area,

$$dQ/dt \sim L^2 L^{1/3} \sim L^{7/3} \sim W^{7/9}.$$

Converting the relationship to fit the present context,

$$dQ/dt \sim L^2 L^{1/3} \sim W^{0.67} W^{0.11} \sim W^{0.78}.$$

The resulting exponent, though indicating change at a rate less than unity, is considerably larger than $W^{0.52}$ estimated in the present study. One possibility of adjustment is offered by the fact that Clark and Phillips (1952) estimated the length–weight relationship for *E. mordax* in southern California to be $W = 0.000269 L^{3.4529}$.
Assuming this relationship to be more appropriate than $W \sim L^3$, we can write

$$dQ/dt \sim L^2 L^{1/3} \sim W^{0.58} W^{0.10} \sim W^{0.68}.$$

The estimated exponent, $W^{0.52}$, is still noticeably lower than this adjusted value but not too far removed from $W^{0.58}$, which pertains only to the area of the mouth opening. The remaining discrepancy could simply be a matter of experimental error. On the other hand it may mean that the true relationship is not satisfactorily explained by the above model. In any event, the true exponent of W is clearly less than unity and mouth opening is probably the dominant factor.

In particulate feeding, the results of the experiment suggest that capacity might influence the relation between feeding and fish weight in the sense that rate of attack may be governed partly by relative fullness. Mouth size, though it may limit the size of prey that can be captured, is not pertinent because it greatly exceeds the size of adult *Artemia*, which are nevertheless usually captured one per bite. Swimming velocity, on the other hand, may exert an effect through rate of contact with food organisms.

Isaacs, (1965) under the assumptions given above, stated the obvious case that where food intake is not related to swimming ability but only to volume capacity, the relation should be

$$dQ/dt \sim L^3 \sim W.$$

Since capacity is a volume factor and appeared to be linear with weight in the present study, the length–weight adjustment as made previously is not appropriate here, and Isaacs' model is applicable as stated. If food intake is influenced by swimming speed as well as capacity, however, the relation presumably should be

$$dQ/dt \sim WL^{1/3} \sim WW^{0.10} \sim W^{1.10}.$$

The empirical estimate from the present study, $W^{1.13}$, is not different from either of these a priori values. Though it is not possible to show whether swimming ability plays a part, the fact that density over the range of 1–25 organisms per liter did not appreciably affect feeding rate suggests that time spent traveling between food particles was not one of the major factors governing food intake. Whether or not swimming ability exerts an influence, it appears that the true exponent of W is approximately unity and that volume capacity of the alimentary tract is the major contributing factor, at least when food is plentiful.

APPLICATION OF LABORATORY OBSERVATIONS TO FEEDING AT SEA

Observations of fish behavior in the laboratory should ultimately be related to the situation in the sea. Information on the feeding habits of *E. mordax* in nature is limited to some casual observations of stomach contents. Allen (1921) examined a few specimens and reported that they contained only diatoms and dinoflagellates. Baxter (1967) reported that *E. mordax* may be predatory on small fish and observed 1.5-inch fish in the stomachs of 5.5-inch anchovies. In a few freshly caught specimens, we found zooplankton and phytoplankton in the digestive tracts but phytoplankton dominated. These observations indicate that *E. mordax* is omnivorous in nature, being a predator at times and a filter feeder at others.

Estimates of the nutritional requirements of the Japanese anchovy (*Engraulis japonicus*) and of the standing crop of plankton off the southern California coast, when considered in relation to the filter-feeding rates determined in this study, suggest that *E. mordax* cannot subsist by indiscriminate filtering in the sea. The daily food requirements of *E. mordax* are unknown but Takahashi and Hatanaka (1960) have estimated that young *E. japonicus*, weighing 1.4–7.3 g, would have to consume 7.8–9.5% of their body weight of *Euphausia pacifica* per day to satisfy their daily requirements. If *E. mordax* is presumed to have the same food requirements, and the midpoint, 8.6%, is taken as the quantity needed, a 4-g fish would need about 344 mg wet weight of euphausiids per day. Lasker (1966) determined that the dry weight of *E. pacifica* is 17.2% of its wet weight. From this figure we tentatively estimate that a 4-g specimen of *E. mordax* needs 59 mg dry weight of plankton material per day.

Special samples taken off the coast of southern California in September, October, and November, 1962 (C.P. O'Connell and R. J. H. Leong, unpublished data) provide an indication of the food mass available to the anchovy. Water was collected with a pump (O'Connell and Leong, 1963), towed at 9 knots and at a depth of 5 m at various times of the day. The straining apparatus aboard ship had mesh openings of 100μ. For each location occupied, the dry weight concentration of plankton was estimated from a few samples representing 2–3 m^3 of water collected over a track of 3–5 miles. Figure 7 shows the estimated plankton concentration and month of collection for each of the randomly located stations. Table 8 shows the frequency distribution of the concentrations. The samples were preserved in formalin for several years before measurement, so the estimated concentrations are undoubtedly conservative because of leaching of salts. Lasker (1966) presented data which show that the weight of *E. pacifica* may be reduced by about one-third after long preservation in formalin. The bulk of the pump samples consisted of small zooplankters and, although the percentage loss is not known, it is not likely to be more than the above.

The efficiency of the gill rakers in retaining particles of different sizes is not known for *E. mordax*, but microscopic examination of the rakers suggests that particles smaller than 100 μ in diameter can be retained. Hence the pump samples lack a segment of the potential filter-food biomass. A report by Beers and Stewart (1967) provides an estimate of the missing segment. They sampled the microplankton (organisms passing through 202-μ mesh) in the euphotic zone at five stations across the California Current east of San Diego. The areas they sampled are relatively oligotrophic but except for the most seaward station are well within the range of *E. mordax*. They also sampled with a pump but strained the water serially with 202-, 103-, and 35-μ cloths. In addition, they took samples of water passing through the 35-μ cloth to estimate the quantity of smaller material. They also estimated the percentage contribution of microzooplankton, phytoplankton, and detritus in each size fraction. These were derived from data, available at the Institute of Marine Resources,

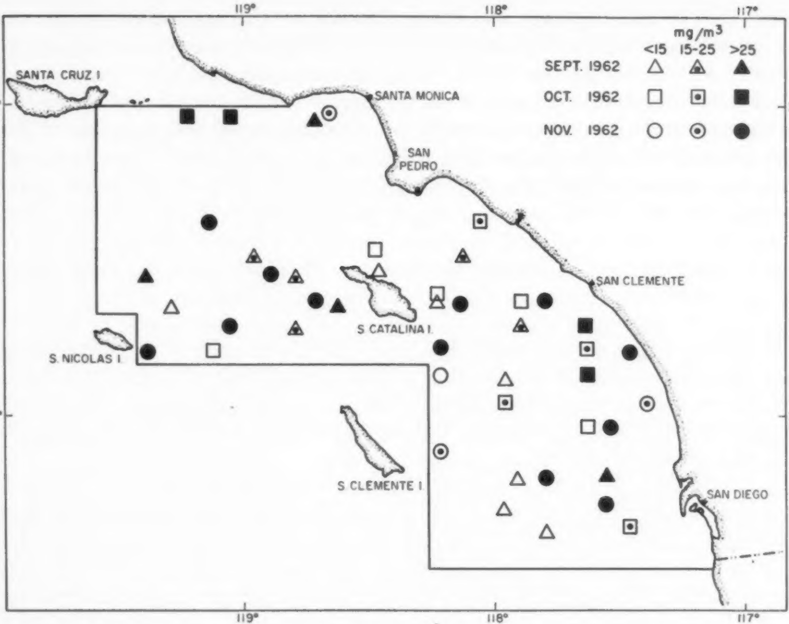
119°
118°
117°
34°
33°
mg/m3
<15 15-25 >25
SEPT. 1962
OCT. 1962
NOV. 1962
SANTA CRUZ I.
SANTA MONICA
SAN PEDRO
SAN CLEMENTE
S. CATALINA I.
S. NICOLAS I.
S. CLEMENTE I.
SAN DIEGO

FIG. 7. The locations of pump sample stations for cruises in three consecutive months of 1962. Stations were selected at random from a grid within the 6000 square mile area outlined. Plankton concentrations are indicated for each station as milligrams dry weight of plankton per cubic meter of water strained.

TABLE 8. Filtering volumes and times necessary to obtain daily ration for observed concentrations of plankton.[a]

A: The anchovy retains only planktonic organisms larger than 100 μ in diameter				B: The anchovy retains all planktonic organisms			
Concn (*mg/m³*)	Frequency observed	Vol (*m³*)	Time (*hr*)	Concn (*mg/m³*)	Frequency observed	Vol (*m³*)	Time (*hr*)
10	14	5.9	75.5	38	14	1.6	20.5
20	12	2.9	37.1	48	12	1.2	15.3
30	15	2.0	25.6	58	15	1.0	12.8
40	3	1.5	19.2	68	3	0.87	11.1
50	1	1.2	15.3	78	1	0.76	9.7

[a] The first two columns in parts A and B show the frequency distribution of plankton concentration estimated by pump samples. The third and fourth columns in A and B show the estimated water volumes that a 4-g anchovy must filter and the time required to obtain 59 mg of plankton.

University of California, San Diego, Calif., on the dry weight of the total particulate matter, the numbers and volume of the microzooplankton, and chlorophyll *a* measurements. Since our pump samples were strained through 100-μ screening and are assumed to be representative for all organisms above this diameter likely to be captured by filtering, only that portion of Beers and Stewart's samples below the 103-μ level is considered here. From their data we estimated that the dry weight concentrations of materials passing through the 103-μ cloth were:

Material	Microzooplankton	Phytoplankton	Detritus
mg/m³	2.9	25.1	270

The above figures are averages of their stations. It is necessary to point out that over 95% of the phytoplankton and detrital material that passed through the 103-μ cloth also passed through the 35-μ cloth. In fact, the combined concentration of phytoplankton and zooplankton retained by the 35-μ cloth was only about 0.5 mg/m³.

From these various estimates of the filter food biomass it is possible to calculate the volume of water and the number of hours that a 4-g anchovy, filtering at the previously determined rate of 78 liters per hour, must strain to obtain 59 mg dry weight of plankton. Since the efficiency of the gill rakers is not known, time and volume was determined for two possible situations. In the first, *E. mordax* is assumed to retain only those particles which do not pass through a 103-μ cloth and the pump estimates of O'Connell and Leong (Fig. 7, Table 8A) are appropriate. In the second, *E. mordax* is assumed to be capable of retaining all plankton, and the 28 mg for combined zooplankton and phytoplankton passing through the 103-μ cloth from Beers and Stewart must be added to the above pump estimates (Table 8B). The addition provides only a rough approximation because Beers and Stewart sampled at a different time and from several depths, whereas we sampled from only a single depth.

Table 8A shows that a 4-g anchovy could not obtain the required quantity of plankton by filtering continuously for 24 hr at most locations off southern California if it utilized only organisms 100 μ and greater in diameter. This implies, of course, that the fish could not survive by filtering randomly over the area as a whole and the implication stands even if the filtering times are reduced by one-third to compensate for a possible underestimate of concentration from the effects of formalin preservation. Since the 35-μ net of Beers and Stewart retained a relatively negligible quantity of phytoplankton and zooplankton, the statement can probably be extended to that level.

The presence of small phytoplankters in the alimentary tracts of *E. mordax* taken from the ocean indicates that the species can utilize at least part of the biomass that passes through a 35-μ cloth. If it is assumed that even the finest particles that pass through such a mesh are retained by *E. mordax*, a 4-g fish would still have to filter more than 14 hr per day in most areas (Table 8B). The assumption of total retention may be unrealistic, however, and *E. mordax* may retain only some unknown portion of such small organisms. If, in addition to the above considerations, it is recognized that some time is required for activities other than feeding, that an individual in the center of a school may encounter water partly cleared by those ahead, and that we sampled from relatively rich waters, it is reasonable to hypothesize that *E. mordax* cannot sustain the daily food requirement by indiscriminate filtering over the area shown in Fig. 7 — although it might be able to do so in limited zones of heavy plankton concentration.

If the anchovy cannot achieve the required daily ration by random filtering over a large area, it is either restricted to zones of high plankton density or will often use the biting attack when a large organism is encountered. The information presented here on particulate feeding suggests, furthermore, that dense aggregations of such large organisms would provide the fish with opportunities to obtain its daily requirement and more in a very short time. The role of particulate feeding cannot be satisfactorily appraised, however, until the relative dispersion of "large" and "small" organisms in the sea, and the response of the fish to mixed size assemblages, are better understood.

One factor that could alter this hypothesis is the role of suspended detritus. Beers and Stewart 1967 found large concentrations of detritus in their samples — more than 300 mg dry weight per cubic meter of water strained at some stations. Fox et al. (1952) also found large concentrations of detritus off San Diego and they concluded "It would be unlikely that the mass of living cells, even of phytoplankton, should exceed that of suspended detritus..., save for relatively brief periods." The nature of filtering behavior suggests that the anchovy cannot avoid the detrital material even if it responds only to the microplankton. If *E. mordax* can retain and utilize the detritus with moderate efficiency, the volume of water that must be filtered to obtain the daily ration would be drastically reduced. The nutritional value of detritus, however, is still in doubt (Jorgenson, 1966), and more research is needed on this potential food source.

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Feeding Behaviour of Cod (*Gadus morhua*)

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Cod 5–90 cm long in captivity used sight to detect food in midwater. Movement of food stimulated feeding but was not essential when feeding on familiar foods. Adult cod could detect and capture falling food down to 2 mm in diameter. Large pieces of food on the bottom were found by sight but smaller pieces were taken after being detected by taste buds on the trailing barbel and pelvic fin rays. Cod were able to detect odours from many live, intact algae, invertebrates, and fish. Food below gravel or stones was located by smell and uncovered by carrying away gravel in the mouth or by rolling stones aside with the head. Food covered by sand was not found. Some live food was captured in the dark. Cod groups fed more effectively than single cod as food deeply buried was uncovered by several fish digging in the same place; food too large for one fish was pulled apart between fish and feeding behaviour by one fish attracted others to the vicinity of food. Thus shoaling of cod may be advantageous to the species by enabling more food to be obtained from a given area.

Larval cod reared from eggs first fed 4 days after hatching. Moving particles were followed by eye movements and captured by swimming forward and snapping if the particles moved in front of the head. Eight days after hatching the cod larvae began to feed on fine stationary particles by removing them from the respiratory water flow.

Received September 16, 1968

INTRODUCTION

Cod have seldom been seen feeding in nature and although examination of stomach contents yields information about the composition of the diet it does not reveal the sequence of events leading up to the detection and capture of the prey. An understanding of the senses employed in the detection of food and of the behaviour patterns used to secure it is necessary to appreciate which factors are likely to be limiting in a given environment. A few observations of this kind have been made with wild cod such as those by Hansen (1949). He reported that cod feeding on capelin will take a bright jig near the surface, suggesting that in such circumstances the cod are feeding mainly by sight.

In captivity, cod remain healthy and feed well enough to grow so their feeding behaviour may be studied in the aquarium. Such studies by Blegvad (1915) showed that cod are able to remove the shells from large molluscs

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Printed in Canada

by seizing the soft parts and shaking the animal out of its shell. McKenzie (1938) found that cod cannot open their jaws widely at temperatures below 2 C and this limits the size of food taken. Captive cod also are strongly attracted to food falling through the water (Bateson, 1889–90; Fulton, 1904; McKenzie, 1935).

This report is based on detailed observations of the feeding behaviour of cod of many sizes maintained under conditions made to resemble those in nature as closely as possible. The observations were made in the 3 years 1954–57 on long-established groups of fish so that the cod were accustomed both to captivity and to each other and took food readily. These observations were supplemented by shorter experiments designed to elucidate such points as the sensory basis of a response which could not be determined by observation alone.

GENERAL METHOD

Cod from the North Sea were kept at the Dove Marine Laboratory in groups of similar sized fish which will be referred to as small (5–18 cm), medium (20–45 cm), and large (45–90 cm). The large and medium cod were kept in separate glass-fronted concrete tanks in water 130 cm deep lit from above by natural light. Water was renewed at night and showed seasonal changes in temperature which in 1956, for example, varied from a minimum of 2 C in February to a maximum of 16 C in July. The small cod were observed in glass tanks 91 × 30 × 30 cm with sand or gravel bottoms in which the water was continuously renewed. During the 3 years 1954–57 of the study the group of large cod contained 6–13 fish, the medium cod group 4–7 fish, and the small cod group usually three glass tanks containing 4–6 fish each, replenished as needed by other small cod from stock tanks. Further details of the aquaria are given by Brawn (1961). The photographs are of cod caught and photographed at Dartmouth, N.S. in 1968.

The feeding behaviour of all three size groups was observed repeatedly during the 3 years. The small cod were fed daily on chopped mussel, except on Sunday, by the observer. The medium and large cod were fed on herring or limpets at irregular intervals of about 2 weeks and much more frequently when feeding behaviour was being examined.

The food, cut into small pieces, sank slowly through the water and any pieces not taken came to rest on the bottom. Each feeding period thus began with falling food but after the first minute both falling food and food resting on the bottom were present, the period ending with all remaining food on the bottom. To evoke digging behaviour food was buried below sand or gravel in the small cod tanks and hidden beneath gravel in a bucket which was lowered into the large cod tank.

In the following account behaviour which was seen and was identical in all cod groups is given without specifying cod size. Fish sizes and numbers are given for the short-term experiments used to determine the sensory basis of the observed responses. The method used for each of these experiments is given in the relevant section. The general descriptions do not apply to cod larvae; these were obtained from spawnings in captivity, and their behaviour was observed in glass bowls under a binocular microscope.

FEEDING IN MIDWATER

General Description

Cod of all sizes studied took food falling through the water in preference to food on the bottom and were able to seize food floating at the surface. On sighting food, the cod tensed the median fins and braked, turned, or increased speed with such co-ordination that the food was rarely missed. This behaviour could be initiated by sight alone such as when a fingertip was drawn slowly through a film of moisture on the glass front of the tank. The cod followed the finger movement with great accuracy, stopping, turning, and reversing direction as necessary. When the fingers were moved from in front of the snout to one side or up and down, the cod followed the movement, not with its eyes, but by a slight movement of the head followed by a movement of the body so that the fish again faced the object. With the snout touching the 1-inch-thick glass the cod was still able to bring both eyes to bear on the object and moved the head up and down in time with the finger movements. This suggests the cod has no blind spot in the midline and sight could guide the fish right up to the moment when food is taken into the mouth.

EFFECT OF FOOD SIZE

Large cod would move toward and follow a 4-mm sphere presented outside the glass front of the tank. The response was soon lost as the fish were not fed. To reinforce the feeding response and determine the smallest object to which the group of 13 large cod would respond discs of 10, 8, 6, 4, 2, and 1 mm diam were stamped out of the opaque mantle of mature mussels and presented to the fish. The discs were introduced singly on the tip of a knife swept through the downward current caused by an aerator. The discs took approximately 1 min to reach the bottom of the 1.3-m deep water layer. The distance of the cod from the food at the moment when tensing the fins or making a fast turn showed the food had been sighted was estimated. The time between introduction and food capture was recorded. The next introduction followed immediately. The series ended with a sweep of the knife through water without adding food. The complete series was repeated 10 times. At the time of the experiment, the tank was lit from above through a window by light from a clear sky and the water was clear.

TABLE 1. Effect of food size on the midwater feeding response of a group of 13 large cod. No responses were given to the mock introductions.

Food disc diam	Discs captured out of 10	Greatest distance disc seen	Avg time disc present before being taken
mm		*cm*	*sec*
10	10	91	8
8	10	61	9
6	10	76	11
4	9	61	18
2	3	46	28
1	1	15	17

The cod, in 12 m^3 of water, missed only one of 40 discs 4 mm or more in diameter but detected and captured few of the 2- or 1-mm discs (Table 1). In a separate test in which 4-mm discs of mussel and filter paper were presented 53% of the 15 mussel discs were taken against 60% of the same number of paper discs. These tests suggest the response is based on vision rather than smell and that food items less than 2 mm in diameter are unlikely to evoke the feeding response from large cod.

EFFECT OF FOOD MOVEMENT

Cod approached and attempted to feed on objects which were not food, such as the fingertips and paper discs already mentioned, so long as these objects moved. To determine whether movement was an essential part of the stimulus when the cod were presented with familiar food organisms, the isopod *Idotea*, the amphipod *Gammarus*, and the rag worm *Nerine* were presented to small cod in active and stationary forms. For each test an active live animal was placed in one water-filled test tube, a dead animal of the same species in another tube, and water only in a third tube. The three tubes were placed in a rack and simultaneously presented to the fish by lowering the bottom of the tubes 5 cm below the water surface. If the active animal ceased to move the test was immediately terminated. The cod responded slightly more often to the stationary dead food than the living food, the numbers of times they touched the three tubes being as follows:

Food animal	Living	Dead	Water only
Gammarus	24	31	4
Idotea	20	44	17
Nerine	50	61	1
Total	94	136	22

This result was attributed to the position of the dead food at the bottom of the test tube where it was closer to the cod approaching from below. Thus it seems that when familiar food objects are presented to small cod in midwater they will attempt to feed on them in the absence of movement and of smell. There is no preference for moving food under these conditions.

TESTING CAPTURED FOOD BY TASTE

When fresh and stale pieces of the same food were present in the tank, cod took both into the mouth and rejected the stale pieces. As the texture is likely to be the same it is presumed the discrimination was based on taste. Cod usually turned sharply away after rejecting food.

PREPARATION OF FOOD BEFORE SWALLOWING

Large pieces of food or those of awkward shape were often held in the buccal cavity while small rapid movements of the jaws interspersed with larger movements, such as those used for rejection but with the mouth closed, occurred. Such movements altered the position of the food in the mouth as did the rejection of large pieces followed immediately by chasing and seizing. Sometimes large pieces were spat partly out of the mouth, then taken in again or shaken. All cod given half mussel shells with mantle adhering promptly seized the softer parts and shook away the shell. The shaking involved both head and body in violent lateral movement with the pectoral fins spread and held perpendicular to the body providing resistance against which the head could act. When large cod were given a live whelk, only once was a cod seen to grasp the foot and it was dropped without shaking. The whelk lived unharmed for 6 months in a tank with 13 large cod.

Group Responses

Cod appeared to recognize the actions of another individual associated with feeding and rapidly approached any fish which nibbled, mouthed, shook, rejected food, or dug. If food was available or rejected, the fish began to feed. Small feeding fish followed by larger ones dropped the food they were carrying. A cod which had partly rejected a piece of food because it was too large often swam slowly until another cod seized the food; it then increased speed and so pulled the food apart. All these actions tended to distribute food among the group.

When food was plentiful, cod were sometimes seen to pick up more food than they could swallow and to carry it in the greatly distended buccal cavity. This behaviour was most pronounced in small cod which were seen to carry food for 15 min without rejection, showing that the action was for storage, not testing food. Sometimes the food was swallowed but often it was spat out with the cod and others nearby chasing, seizing, and swallowing the pieces as quickly as possible. Such behaviour would allow cod to obtain the maximum food from a dangerous feeding area in the shortest time and carry it to a safer area for ingestion.

FEEDING ON THE BOTTOM

General Description

Large pieces of food on the bottom were taken by all the cod studied after a fast approach from a distance using the same feeding behaviour as towards food in midwater. Smaller pieces of a size taken readily when falling through the water were overlooked when they settled on the bottom. Such pieces were found by a different behaviour not based on sight and which was shown only when food odour was present but no food visible in midwater. This bottom feeding behaviour could be evoked by introducing food odours into water flowing into the tank. It was not shown by a cod with nostrils recently blocked (see below) even when food was on the bottom although this cod still fed readily on food in midwater.

After taking all the falling food cod swam downwards and moved erratically just above the bottom with the free tips of the first two fin rays of the pelvic fin and often the distal half of the barbel trailing over the surface (Fig. 1). The pelvic fins were held out from the body so as to touch the bottom at some distance on either side of the fish. If either the barbel or the pelvic fins touched food, the fish immediately stopped, backed, and fed. When backing to reach food touched by one of the pelvic fins, the fish did not turn toward the pelvic fin which had been stimulated. Food was captured by moving straight backwards combined with large lateral movements of the head which continued until the trailing barbel made contact with the food. Moving the head slightly from side to side, the cod ran the barbel over any food it touched, whether it had just been located or found first by the pelvic fins. If acceptable, the food was sucked from the bottom in a stream of water flowing into the rapidly opened mouth. If the first attempt to draw in food was unsuccessful the cod assumed a head down position and by movements similar to respiratory movements but more rapid and intense drew a current of water in through the mouth and out through the gills until the food was sucked in.

SENSORY DISCRIMINATION BY BARBEL AND PELVIC FINS

The innervation and sensory structures of the barbel and pelvic fins of the cod were examined by Herrick (1900, 1907). He did not examine the sensory capabilities of living cod but based on work with *Urophycis tenuis* and *Microgadus tomcod*, which seek food on the bottom in the same manner as cod, he concluded that although the response of seizing food was usually initiated by tactile and gustatory stimuli acting together, the gadoids can respond to taste alone. The innervation of the taste buds on the free pelvic fin rays of cod is through the facial nerve. Evans (1935) and Kappers et al. (1936) also mention this innervation.

To extend Herrick's observations to the cod, a 64-cm female cod which had been in captivity for 2 years was deprived of its sense of smell by blocking the nasal cavities with vaseline. The fish showed no bottom feeding behaviour until trained to do so by dropping large pieces of food which could be found by sight among smaller pieces of food on the bottom. This training and accustoming the fish to the conditions of the experiment took 3 weeks. To test the ability of this cod to distinguish objects by taste using the barbel and pelvic fin rays, the cod was presented with identical 10-cm square glass fabric bags, one filled with mussel and the other stuffed with glass fibre. Eleven presentations each lasting 5 min were made with the positions of the two bags reversed for each presentation. The bags were flattened on the bottom with a rake. Every contact of barbel or pelvic fin with a bag and the numbers of feeding responses (backing up, whether with or without a bite at the bag) were recorded. In the 55-min period the numbers of responses to contact with the two types of bags, according to receptive area, were:

Stimulus	Mussel-filled bag		Padded bag	
Receptive area	Barbel	Pelvic fin	Barbel	Pelvic fin
Feeding responses	14	28	0	0
No response	6	7	25	12

The cod never responded to the tactile stimuli from the padded glass fabric bag even in the training period and in this respect differed from the gadoids studied by Herrick which had to learn to disregard tactile stimuli alone. The occasional failure to respond to the mussel-filled bag may be due to the lack of gustatory stimuli at the surface especially near the seams where the material was several layers thick.

Gustatory discrimination by the pelvic fins and barbel seemed to be less precise than this sense in the mouth. Ten pieces of formalin-treated mussel given to the anosmic cod all caused the backing response when touched by fins or barbel and eight pieces were taken into the mouth. Of these, seven were subsequently rejected. One 11-cm cod also picked up formalin-treated mussel after touching it with the barbel but rejected it from the mouth.

FEEDING ON BURIED FOOD

Digging Response

The digging behaviour of small cod was examined by hiding small pieces of mussel at various depths below 1-cm diam gravel so that the mussel was against the glass front of the tank. The observer was screened from the tank.

In the vicinity of the buried food, the fish became alert, raising all median fins fully. Moving down to the stones, the fish began to search for the food, moving back and forth rapidly just above the bottom. The pelvic fins were not dragged over the surface as in food seeking on a sandy bottom, but gently tapped the surface of each pebble. The barbel was used to investigate the surface of stones and especially as a probe between them. It precedes the head during digging and so is the first part of the body to come into contact with the food.

To dig, the small cod inclined its body steeply and made rapid side-to-side movements of the head driving the snout between stones (Fig. 2). The snout is wedge-shaped making it an effective instrument for digging. While digging the pectoral fins beat alternately with great rapidity accompanied by fast beats of the tail forcing the head downwards. Pebbles as large as the cod's head anterior to the eyes were lifted bodily during digging. Small fish sometimes seized a pebble in their mouths and tossed it to one side. Bites which sometimes occurred while the head was in a crack but before the barbel touched food helped to move the stones apart.

Digging movements occur with surprising accuracy. Once when food was hidden one pebble deep, it was uncovered by three thrusts of the snout all directed against the one pebble on top of the food. Food buried 3 cm deep below 3 layers of pebbles was not uncovered by the small cod in 24 hr although they dug vigorously. In 35 min the longest period of continuous digging was 2.0 sec with periods of 0.6 sec or less being common.

Loose pieces of food were sucked in before the cod had dug down to their level during the occasional bites. Digging continued for a while after all the food had been found and eaten and occurred when the food was completely hidden and inaccessible suggesting the smell of food alone arising from between pebbles will initiate digging.

Large cod given food hidden in a bucket of 1–3-cm gravel rarely used sideways thrusts of the head to push aside the pebbles but made violent bites above the food, sucking in some of the gravel and holding it in the mouth for a moment before rejecting it a short distance away. Individual cod soon gave up the attempt to reach food but a succession of cod, all removing some of the gravel, cleared the way for the cod that eventually was successful. The depth at which buried food could be uncovered thus depended on the number of cod attracted and the time each spent sucking up pebbles. Both of these factors presumably depend on the strength and attractiveness of the odour from food. Large cod pushed rounded stones 10–25 cm in diameter to one side with the snout or rolled them over by snapping violently once the snout was below the stone and so obtained food placed below the rock. One 47-cm cod was seen to move a stone to one side which weighed 3600 g and was roughly 24 × 12 × 7 cm. With stones this size, the behaviour of the large cod was the same as that seen in the small cod digging in gravel.

Cod seem unable to find food buried below sand in the absence of any opening to bring odours to the surface. Four 15-cm cod were given mussel buried under $1\frac{1}{2}$ mm of sand, the thinnest possible complete cover. Not even the general area in which the food had been buried was found in the first 45 min and the food was still present 24 hr later.

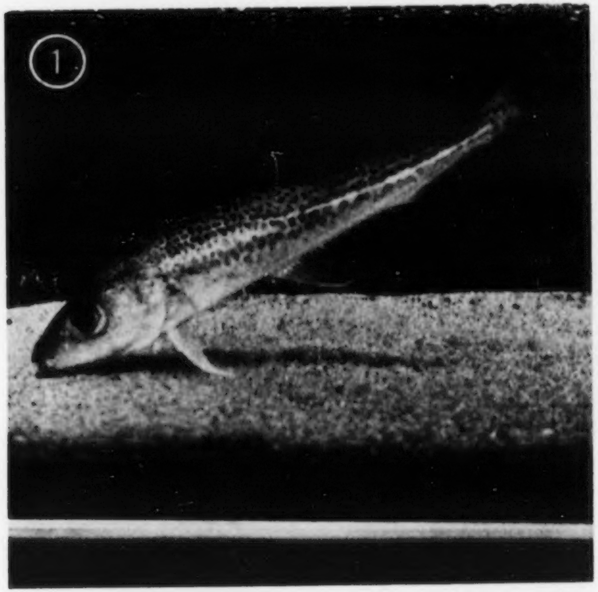
RESPONSE TO ODOUR

To establish which odours and their concentrations could be sensed by cod would require a series of conditioning experiments but an indication of the cod's ability to detect odours is given when a change in behaviour occurs after the introduction of an odour without altering any other physical parameter. The response given may be innate or may have been learned during the time the cod was at liberty before capture. In such tests a negative result has little significance but a marked change in behaviour suggests that the cod can sense the odour introduced.

METHODS

The cod were kept singly in a rectangular tank screened from the observer and all parts of the apparatus which had to be manipulated. In one corner of the tank was a cover under which the cod could hide. In the corner diagonally opposite the cover, water was continuously introduced and seeped up into the tank through a pile of gravel (Fig. 3). Clip A was adjusted until the water pressure filled each pot to the 1320-cc level and stopped there when its clamp was removed. At this setting, it was possible to introduce water from any pot into the inflowing stream by removing the appropriate clamp C and putting on clamp B. The flow rate from the pot would initially be 172 cc/min, the same as the usual incoming stream, falling to 160 cc/min at the 320-cc mark, a reduction of no more than 7% of the normal flow.

Prey animals to be tested for odour were injury-free and were rinsed in sea water to remove silt. As odour from human skin would invalidate the results precautions were taken to see that neither the containers nor prey were handled. To prepare the test solution each pot was filled to the 1200-cc mark by opening clamp C. A known volume of live prey was then added to the pot.



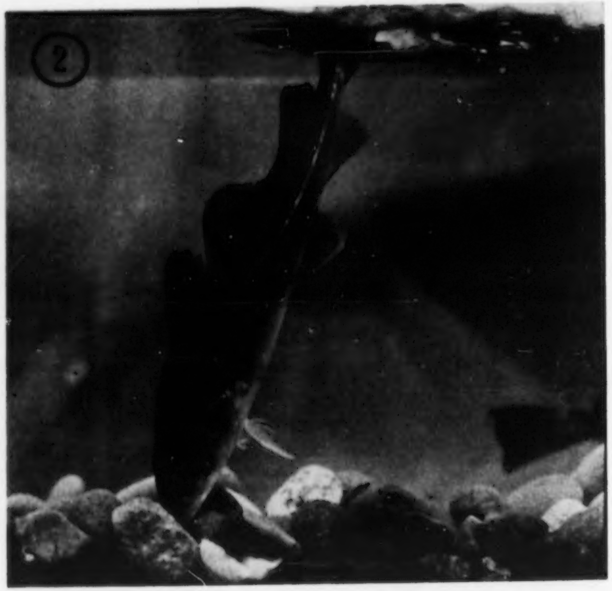


FIG. 1. Bottom feeding behaviour by a 20-cm cod.

FIG. 2. A 27-cm cod beginning to dig for a slice of herring (*arrow*). The whirlpool at the surface shows the effort the cod exerts to dig. The food was uncovered after several digging attempts by moving apart the two stones immediately to the right of the cod's head.

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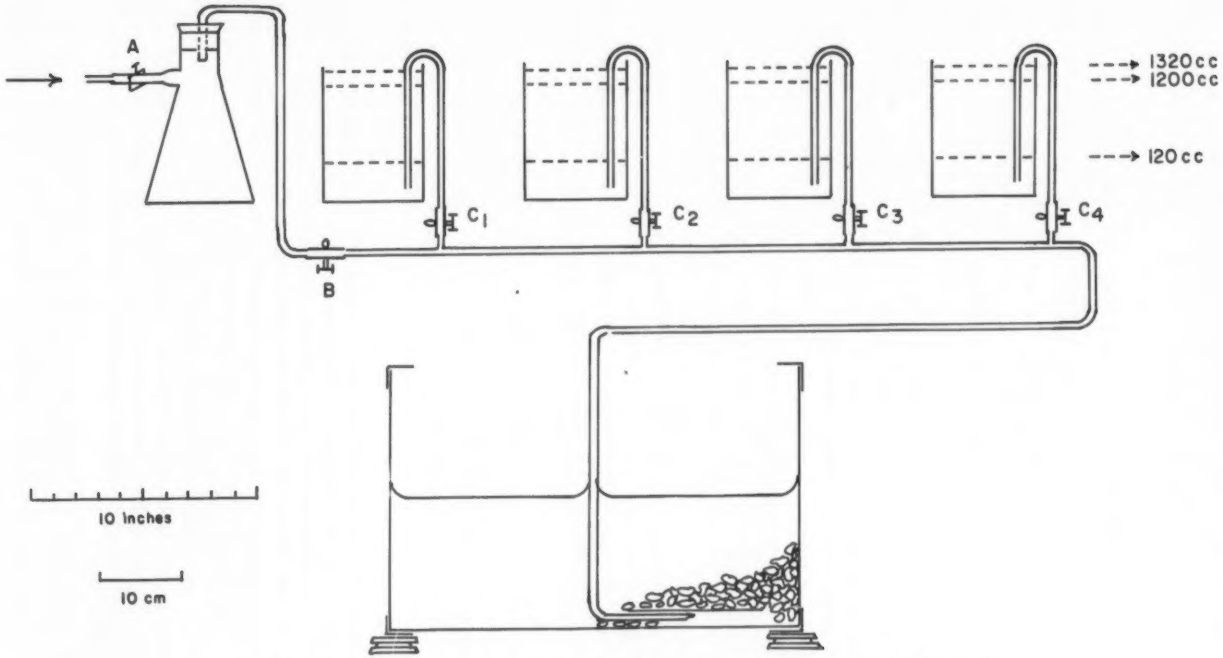
A
B
C1
C2
C3
C4
1320 cc
1200 cc
120 cc
10 inches
10 cm

FIG. 3. Vertical section of apparatus used to investigate odour perception by cod.

This volume and the time during which prey was in contact with the water before the test are given in Table 2. Hand rinses were prepared by rubbing the palms together in 1200 cc of sea water for 1 min. The hands were scrubbed with a brush without soap 1.5 hr before preparing the rinse. The rinse was immediately presented to the fish.

TABLE 2. Response of 16-cm cod A (first entry only) and cod B to odours.

Material	Test solution Amount (*ml*)/ seawater volume(*ml*)	Time	Digs	Crosses inflow(%)	Remarks
Hand rinse	2 hands/1000	1 min	32	97	Marked attraction
Nerine cirratulus	10/1200	2 hr	0	87	Vigorous search
Hand rinse	2 hands/1000	1 min	9	81	Marked attraction
Conger eel skin extract	50 cm^2/1000	–	16	79	” ”
Hand rinse	2 hands/1000	1 min	6	74	” ”
Corrallina officinalis	100/1200	2 hr	0	71	Moderate attraction
Actinia equina	120/1200	2 hr	0	64	Moderate attraction
Grantia compressa	10/1200	2 hr	0	64	Short attraction
Arenicola marina	50/1200	24 hr	0	61	Moderate attraction
Ulva lactuca	120/1200	2 hr	0	51	” ”
Cardium edule	120/1200	2 hr	5	50	” ”
Cancer pagurus	120/1200	2 hr	0	48	Long search
Repulsion					
Trachinus vipara	2 fish/1200	2 hr	0	55	Delayed avoidance
Centronotus gunnellus	120/1200	2 hr	0	46	Attempted escape
Hyas araneus	120/1200	2 hr	0	45	” ”
Cottus bubalis	120/1200	1½ hr	0	38	” ”
Cottus bubalis	100/1200	2 hr	0	36	Inflow avoided
Zoarces viviparus	60/1200	1 hr	0	26	Attempted escape
Pleuronectes platessa	60/1200	2 hr	0	18	Fish uneasy
Zoarces viviparus	120/1200	1 hr	0	16	Pauses

The movements of cod were recorded on a plan of the tank bearing a grid equivalent to the grid of 4-inch squares above the tank. Each test started with a 1-min record of the movements and behaviour of the undisturbed cod. Two minutes later clip C was released and clip B closed. Observations began 30 sec later as tests with dye had shown more than 30 sec elapsed before water from any of the pots entered the tank. The route of the fish was recorded for 6 min. The number of times the fish dug among the rocks, attempted to swim through the far side of the tank, or showed an avoiding reaction near the rocks were noted.

Each test was separated by at least an hour from the preceding test. Control tests were carried out by presenting sea water which had stood in the pots up to the 1320-cc mark for a known number of hours. These controls were necessary to assess whether slight changes in temperature or gaseous content of the standing water or any of the manipulations were affecting the behaviour of the fish.

Most tests were made on two 16-cm cod (A and B) which had been in captivity for 1 year. When these cod showed a strong attraction to hand rinses two 10-cm cod (C and D) were captured and were not given the opportunity to associate human odour with food. These newly caught cod were then tested for their response to human odour.

RESULTS AND CONCLUSIONS

Before the test the cod usually circled the tank slowly and crossed the diagonal from cover to inflow about an equal number of times in each half of the tank. Before the tests, the crossings in the inflow half were 58% for fish A and 50% for fish B. Cod A and B showed marked attraction to hand rinses, and cod B to conger eel skin extract and *Nerine* bringing the percentage to 75 or more (Table 2). Newly caught fish C and D which had been given no opportunity to associate human odour with food responded to the first hand rinse by faster swimming, quick turns, and head shaking. A second presentation caused the same response followed by vigorous digging and one attempt to feed on bubbles. Thus it appears cod are attracted to human odour in its own right. A more moderate attraction was shown by cod B to odours from invertebrates of many phyla. In addition to the invertebrates shown in Table 2, the cod apparently sensed and showed momentary interest in odours from *Ceramium rubrum*, *Eupagurus bernhardus*, and *Eledone cirrhosa*. These results suggest that some intact, live invertebrates and algae produce odours which are sensed by and attract cod. During the tests, the cod failed to respond to nine invertebrate species but this may not be significant so these results were omitted from the table. No response was given to the introduction of standing sea water which served as a control.

The odours which caused avoidance reactions all came from fish with the exception of *Hyas*. For young cod this may be a reaction which removed them from the vicinity of predators but the ability to detect fish by odour may be significant in feeding behaviour of older cod which change from an invertebrate to fish diet.

When 1280 cc of water in which 40 ml of *Halichondria panicea* had been standing for 19 hr was introduced, the cod showed no response although this material killed the fish within 7 hr. The toxicity of this sponge to fish was confirmed by a further test in which an 8-cm long rough dab in a similar solution died within 5 hr.

FEEDING IN THE DARK

Bateson (1889–90) lists cod among fish which are unable to feed at night or even in dim light. McKenzie (1933) observed 22–32-cm cod in captivity and concluded that normal cod feed by sight and all feeding occurs in daylight. He noted that a totally blind cod became aware of its food by touch, thereby suggesting a method by which cod might feed during darkness. The relation of stomach weight to body weight of young cod caught at different hours was determined by Blegvad (1917). The ratio was 1:60 at 5 PM, 1:137 at 9:30 PM, but became 1:40 the following morning before sunrise suggesting cod of the 0–II group also feed at night.

One 13-cm cod in 42 liters of water in a darkroom for 17.5 hr captured all the living organisms in its tank. These were 10 *Gammarus* and 10 *Nerine* freshly collected and selected for freedom from injury. *Nerine* and perhaps

Gammarus could be detected from a distance by smell and may have been captured on the bottom after being sensed by the taste buds on pelvic fin or barbel.

FEEDING BEHAVIOUR OF LARVAL COD

Two types of feeding behaviour were observed in larvae resulting from three spawnings by captive cod. The first began on the 4th day after hatching when eye and jaw movements were seen for the first time. It could be evoked by moving a hair tip within a head's length of the head of the larva. When the tip was at the side of the head and moved towards the midline, it was followed by the eye. The cod by vibrating the pectorals and tail swam forwards and snapped at the tip once it reached the midline. The larvae were seen to capture discrete particles in the water by this means, especially particles which were moving. When the particles were inedible, the larvae withdrew with head shaking. From the 5th day onwards, similar behaviour was used to space out the larvae. Any larva coming within one body length of another, paused, extended and vibrated the pectoral fins, and then swam rapidly towards the other larva and either snapped or bumped into it. The attacked larva responded by swimming away.

The second type of feeding occurred while the larvae were not swimming and was not shown until 8 days after hatching. When the larvae were not feeding small particles could be seen to pass in and out of the mouth with each respiratory movement as the mouth was not completely closed. When fine fragments of mussel mantle were added to the water, the rate of mouth closing almost doubled and the mouth was closed more completely until all the particles which entered the mouth were retained. This mode of feeding was shown toward fine, stationary particles.

Up to the 18th day, the larvae showed no feeding response to ciliates even when these ran over the head of larvae. No ciliates were seen in the gut. As the larvae became older, more avoidance responses and few feeding actions were given towards the hair tip suggesting finer discrimination. No avoidance, however, was shown towards ephyra which were feeding on the larvae. Observations ceased on the 18th day as the larvae were not reared past this time.

DISCUSSION

The behaviour observed here suggests that the tendency of wild cod to occur in shoals may enable them to feed more effectively in a given area than the same population of solitary individuals. Food which is too deep for a single cod to uncover may be exposed when successive cod dig in the same place. Food too large for a cod to swallow may be torn into pieces of appropriate size when other cod seize projecting parts. Since cod rapidly approach any cod which begins to feed, each cod within a shoal acts as a scout for all cod within sight.

All postlarval cod studied showed three distinct types of feeding behaviour according to whether the food was pelagic, on the bottom, or buried. Each type required different information from the environment and so a factor which would limit one type of feeding would not necessarily limit the other types. Pelagic feeding could be limited by low light intensity leading to a diurnal feeding rhythm with little feeding at night. An example of this is given by Trout (1957) for Bear Island cod in water less than 100 fath deep in January to March and in water 150–250 fath deep in April to June. Low light intensity does not prevent all feeding as about 70% of cod from below 150 fath in the winter near Bear Island contain some food which may have been taken from the bottom without the use of vision as little light penetrates to such depths in winter.

The demonstrated ability of cod to move towards the source of odours from benthic invertebrates would be expected to enhance the contranatant movements usually shown by cod near the bottom. In midwater, the source of odours is unlikely to be fixed in space so a cod moving up the odour gradient would not always swim upstream. In addition, the primary sense for midwater feeding is vision so cod are likely to be attracted to food in directions bearing no constant relationship to the current.

ACKNOWLEDGMENTS

This study was made possible by funds granted by the Development Commission of the United Kingdom to Dr H. O. Bull of the Dove Marine Laboratory, England. My sincere thanks go to Dr Bull for his helpful criticism and encouragement. I also wish to thank Dr L. M. Dickie for permitting me to use the facilities of the Marine Ecology Laboratory to prepare the work for publication, and for his comments on the manuscript.

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Structure de la rétine chez quelques téléostéens marins du plateau continental[1]

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Une étude histologique détaillée de la rétine fut entreprise chez 20 espèces de téléostéens pélagiques et benthiques du plateau continental. Quelques corrélations ont pu être établies entre les conditions lumineuses de l'habitat, le mode de vie, et les différentes adaptations de l'appareil visuel de ces poissons. En fonction des conditions lumineuses, certaines composantes rétiniennes sont capables d'une grande variabilité; mentionnons le pigment épithélial, l'abondance et la taille des cônes et bâtonnets, et le développement des couches nucléaires. Superposé aux conditions lumineuses, le mode de vie de ces poissons a une grande influence sur certains aspects fonctionnels du modèle rétinien, tels l'acuité visuelle et la spécialisation topographique des cônes. Il est suggéré que le développement des composantes rétiniennes fut inspiré par des modèles phylogéniques caractéristiques de chacun des grands groupes de téléostéens. Puis au cours de l'évolution, la kyrielle des habitats et des modes de vie a conditionné la formation de variantes écologiques.

ANCTIL, MICHEL. 1969. *Structure de la rétine chez quelques téléostéens marins du plateau continental.* J. Fish. Res. Bd. Canada 26: 597–628.

A detailed study of retinal structure in 20 pelagic and demersal species of fish indicates that valid correlations exist among the photic environment, activity of the fish, and its visual apparatus. Generally, the relative abundance of rods is inversely proportional to that of the cones. This relationship exists inter-specifically in the same retinal region and intra-specifically in different parts of the same retina. The topographical specialization of cones, or formation of a retinal area, is high in active pelagic species (*Clupea, Alosa*), less in sluggish demersal fish, and absent in the shore fish *Tautogolabrus* where a specific ocular behavior compensates. The resolving power of the retinal area is high in pelagic and shore fish, but is lower in demersal species. The distribution of the cone types within a retina suggests that photic sensitivity increases from single to quadruple cones. Cone arrangements are more refined in active species likely to detect fast-moving preys. Inter- and intra-specifically, the development of the inner retinal layers parallels that of the cones. The functional importance of the resolving power appears to rely heavily on the extent of summation at the bipolar and ganglion cell layer level. The cone/rod and single/double cone ratios are proportional to the abundance of bipolar neurons in the species examined.

Received October 30, 1968

INTRODUCTION

L'OEIL DES TÉLÉOSTÉENS est un matériel d'étude particulièrement appréciable en ce qu'il apporte, à ce stade de l'évolution des vertébrés, un grand nombre de structures nouvelles. Non seulement ces structures sont-elles

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[1] Ce travail est extrait d'une thèse présentée à la Faculté des Sciences de l'Université de Montréal en vue de l'obtention du grade de Maîtrise ès Sciences.

Printed in Canada

inédites, mais plusieurs d'entre elles ne passeront pas à l'histoire des vertébrés supérieurs.

Parmi ces éléments d'intérêt, plusieurs ont été retenus par la rétine, siège du processus photosensoriel. Cet organe est capable d'une grande variabilité à l'intérieur d'un groupe taxonomique, comme l'ont montré les travaux des prédécesseurs (voir Walls, 1942). La variabilité des structures rétiniennes chez ces poissons est telle qu'il nous apparaît fort instructif de la relier à des facteurs du milieu, tels l'habitat et le mode de vie. Dans le passé, cet objectif a déjà été atteint chez les poissons marins. Notamment, les poissons épipélagiques (Vilter, 1950; Baburina et Kovaleva, 1959; O'Connell, 1963; Tamura et Wisby, 1963), chez lesquels la rétine est généralement bien développée et cela surtout dans une zone dite d'acuité. Les poissons méso-, bathypélagiques et abyssaux (Brauer, 1908; Contino, 1939; Vilter, 1951, 1953, 1954a, b; Munk, 1963, 1964, 1965, 1966) montrent des adaptations visuelles souvent insolites, telles les yeux téléscopiques à rétine accessoire et la couche visuelle à étages multiples de bâtonnets.

Toutefois, peu de chercheurs ont étudié spécifiquement la rétine des poissons habitant le plateau continental (proximité du littoral et du benthos). Citons les travaux de Wunder (1958) et Hanyu et Ali (1962) sur le sébaste, et ceux de Ali et Hanyu (1963) et Ali et al. (1968) sur toute une kyrielle d'espèces. Chez beaucoup de ces espèces, la conformation rétinienne apparaît intermédiaire en développement entre les poissons à vision photopique et ceux à vision scotopique. Par exemple, l'épithélium pigmenté contient peu de pigment mélanique, le développement des cônes est mitigé, les changements photomécaniques sont réduits, et les couches internes (nerveuses) ont souvent tendance à dégénérer.

A la suite de ces recherches, une étude plus détaillée de la structure rétinienne s'avérait nécessaire chez les téléostéens marins du plateau continental, afin de saisir plus clairement les rapports entre l'environnement (écosystème marin) et la qualité visuelle telle que réflétée par la rétine. Dans cette optique, un programme de recherches fut entrepris chez 20 téléostéens du Golfe St-Laurent. Pour atteindre cet objectif, nous avons insisté sur deux points négligés dans le passé: les coupes tangentielles et leur supplément d'information, et l'importance d'étudier le plus de régions topographiques possibles dans la même rétine.

De plus, l'étude approfondie de l'ensemble de ces éléments est susceptible de nous faire mieux saisir les rôles respectifs de la phylogénie et de l'écologie dans le développement des composantes rétiniennes.

MATÉRIEL ET MÉTHODES

MATÉRIEL

Les recherches ont été effectuées chez 20 espèces marines de téléostéens recueillies dans le Golfe St-Laurent. Ces espèces se répartissent en 10 familles. L'identification des spécimens fut réalisée d'après Leim et Scott (1966). L'ordre de présentation des différentes espèces suit celui suggéré par les mêmes auteurs.

Famille: Clupeidae
Alosa pseudoharengus (Wilson), gaspareau
Clupea harengus harengus Linné, hareng atlantique
Famille: Osmeridae
Mallotus villosus (Müller), capelan
Osmerus mordax (Mitchill), éperlan d'Amérique
Famille: Labridae
Tautogolabrus adspersus (Walbaum), tanche-tautogue
Famille: Stichaeidae
Eumesogrammus praecisus (Krøyer), quatre-lignes
Famille: Zoarcidae
Lycodes lavalei Vladykov et Tremblay, lycode de Laval
Lycodes reticulatus Reinhardt, lycode arctique
Lycodes turneri Bean, lycode polaire
Lycodes vahlii Reinhardt, lycode de Vahl
Lycodes sp.
Famille: Cottidae
Myoxocephalus octodecemspinosus (Mitchill), chaboisseau à dix-huit épines
Myoxocephalus scorpius (Linné), chaboisseau à épines courtes
Triglops murrayi Gunther, faux-trigle maillé
Famille: Agonidae
Agonus decagonus Bloch et Schneider, agone atlantique
Aspidophoroides monopterygius (Bloch), poisson-alligator atlantique
Famille: Cyclopteridae
Cyclopterus lumpus Linné, grosse poule de mer
Famille: Pleuronectidae
Glyptocephalus cynoglossus (Linné), plie grise
Limanda ferruginea (Storer), limande à queue jaune
Famille: Lophiidae
Lophius americanus Valenciennes, baudroie d'Amérique

MÉTHODES

Les spécimens furent capturés dans les eaux littorales de Gaspé-Sud, Grande-Rivière, ou au large dans le Golfe St-Laurent. Les moyens de capture étaient variés (seine, filet maillant, chalut) selon l'habitat et l'espèce considérés. La profondeur à laquelle les spécimens furent capturés est indiquée dans le Tableau 1.

La longueur à la fourche de tous les spécimens traités fut d'abord mesurée, ainsi que le diamètre horizontal (ou temporo-nasal) de l'oeil et le diamètre du cristallin (Tableau 1). Les yeux étaient immédiatement prélevés et énucléés, puis fixés au Bouin pour 48 hr. et transférés dans l'alcool 70%. Avant de procéder plus loin, la rétine était le plus souvent isolée et découpée en plusieurs zones topographiques. Faisant suite au processus d'enrobage à la paraffine, les coupes sériées furent opérées à 6 μ d'épaisseur, transversalement et tangentiellement. Les colorants utilisés furent l'hématoxyline Harris et l'éosine alcoolisée.

Pour les différentes mesures à enregistrer, un microprojecteur Visopan (Reichert) et une règle calibrée furent utilisés. L'épaisseur totale de la rétine (Tableau 1) et l'épaisseur de ses différentes couches sauf l'épithélium pigmenté furent ainsi enregistrées chez les différentes espèces, ainsi que la longueur et la largeur des cônes et bâtonnets. Le nombre de cônes fut déterminé sur des coupes tangentielles pour une superficie de 0.04 mm^2, à l'aide d'un micromètre oculaire quadrillé. Le nombre de noyaux à bâtonnets dans la couche nucléaire externe et le nombre de bipolaires dans la couche nucléaire interne furent comptés selon la méthode de Trowell et Westgarth (1959) telle que décrite par O'Connell (1963), pour une superficie de 0.04 mm^2. Le plus souvent, le nombre de cellules horizontales, amacrines et ganglionnaires fut déterminé linéairement pour 0.2 mm, et ensuite la valeur fut déduite pour une superficie de 0.04 mm^2. Toutes ces mesures se répétèrent pour chacune des zones étudiées (Tableaux 2–6), et ne concernent qu'un seul spécimen adulte, sauf indication contraire.

TABLEAU 1. Données de base concernant les espèces étudiées. Le plus souvent, le diamètre du cristallin indiqué est celui d'un seul individu, principalement étudié. L'épaisseur de la rétine, épithélium pigmenté exclus, réfère aux valeurs extrêmes de la rétine d'un seul individu, sauf pour *Lycodes reticulatus* et *Limanda ferruginea*.

Espèces	Profondeur de capture (*m*)	Longueur à la fourche (*mm*)	Diamètre de l'oeil (*mm*)	Diamètre du cristallin (*mm*)	Epaisseur de la rétine (*μ*)
Alosa pseudoharengus	[a]	340	14.5	5.20	108–346
Clupea harengus	[a]–14	325–350	14–15	6.00	199–305
Mallotus villosus	[a]–120	150–180	6–8	2.94	200–352
Osmerus mordax	[a]	175	6.5	3.07	246–261
Tautogolabrus adspersus	[a]	210–255	8.5–9.0	3.50–4.20	166–264
Eumesogrammus praecisus	100	138	7	2.75	151–239
Lycodes lavalei	80–130	245–640	10.5–14	6.88–7.60	99–178
L. reticulatus	80–130	234–725	7.5–14.5	3.88–7.60	116–229
L. turneri	100–120	115–255	5.2–10	1.80–4.12	106–184
L. vahlii	80–130	226–290	6–10	3.85–4.80	106–189
Lycodes sp.	110–120	600–630	12–17	6.68–6.88	114–195
Myoxocephalus octodecemspinosus	110–120	245–270	13–15	5.84	117–192
Myoxocephalus scorpius	80	240–275	12–13.5	5.10	108–295
Triglops murrayi	80–120	100–130	7–8.5	3.25	92–189
Agonus decagonus	100	220	10.5	3.38	130–185
Aspidophoroides monopterygius	80–130	108–210	3.5–9.5	1.36–3.64	100–196
Cyclopterus lumpus	40–80	290–320	10–12	4.22	184–234
Glyptocephalus cynoglossus	110–120	130–435	5–13	6.70	97–234
Limanda ferruginea	60–120	143–290	6–9.5	2.12–5.07	164–281
Lophius americanus	20–60	690	23	10.60–10.70	124–227

[a] Spécimens capturés dans les premiers mètres à partir de la surface, ou sur la grève dans le cas du *Mallotus* en période de reproduction.

OBSERVATIONS

1. *ALOSA PSEUDOHARENGUS* (FIG. 4, 32–34)

La couche visuelle est particulièrement bien développée. Les cônes y sont bien représentés selon les régions (Fig. 1A), et sont simples, doubles symétriques (= cônes jumeaux) ou doubles asymétriques (Fig. 4). Les cônes doubles dominent, surtout dans certaines zones plus faibles de la rétine. Dans l'area retinae, zone rétinienne à pouvoir de résolution plus élevé (région ventrale), les cônes doubles sont environ deux fois plus nombreux que les cônes simples. L'area retinae de l'espèce parente *Alosa sapidissima* fut localisée par O'Connell (1963) à proximité de la périphérie ventrale, mais temporalement. Une zone désintégrée minuscule est aperçue dans la région du fundus temporal, ou plusieurs cônes triples du type triangulaire (Fig. 34) et quelques cônes apparemment quadruples sont présents.

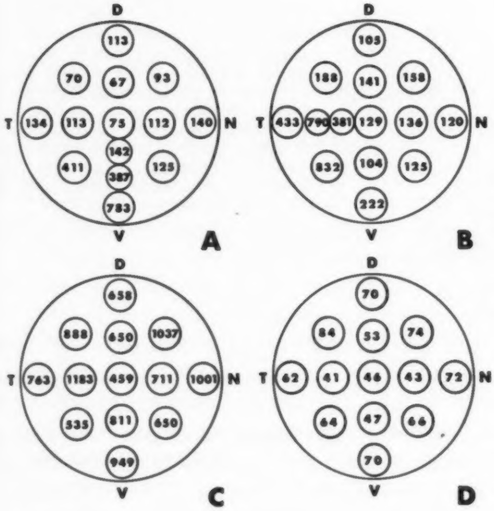


FIG. 1. Distribution de la densité des cônes dans la rétine de quatre téléostéens. A, *Alosa pseudoharengus*; B, *Clupea harengus*; C, *Tautogolabrus adspersus*; D, *Lophius americanus*. D, N, T et V signifient respectivement les régions dorsale, nasale, temporale et ventrale de la rétine. La valeur centrale est celle du fundus.

L'observation des coupes tangentielles montre que la disposition spatiale des cônes change d'une zone à l'autre. Dans les zones rétiniennes avantagées (ventrale, temporo-ventrale), la mosaïque est du type B tel qu'illustré dans la Fig. 2. Il s'agit d'une mosaïque carrelée de cônes doubles avec cône simple central (Fig. 33). Dans beaucoup d'autres régions, elle s'apparente au type F composé de rangées parallèles de cônes doubles. Le type G, qui n'a pas encore été relevé dans la littérature, est trouvé dans la région du fundus dorsal seulement (Fig. 32).

Les bâtonnets sont très nombreux relativement aux cônes. Le nombre de bâtonnets est particulièrement faible dans la région ventrale ou area retinae.

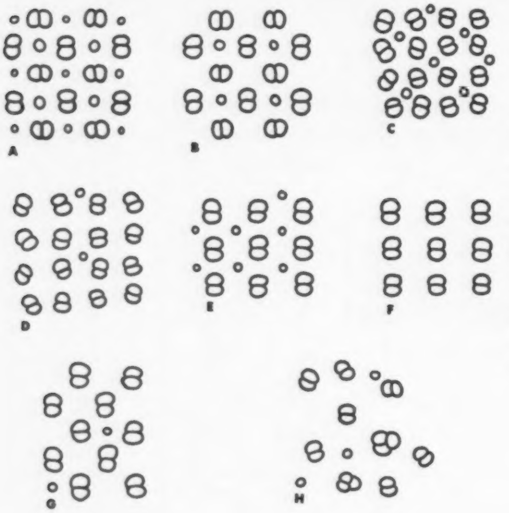


FIG. 2. Représentation schématique des différentes mosaïques à cônes rencontrées chez les téléostéens étudiés. A, mosaïque carrelée à cônes simples centraux et accessoires; B, mosaïque carrelée à cônes simples centraux; C, quadrilatère modifié à cônes simples centraux; D, quadrilatère modifié à cônes simples occasionnels; E, rangées parallèles alternantes de cônes simples et doubles; F, rangées parallèles de cônes doubles; G, rangées parallèles de cônes doubles à orientation modifiée; H, mosaïque désintégrée à cônes simples et triples occasionnels.

Par contre, il y a de 10–20 fois plus de ces éléments dans les autres zones rétiniennes.

La couche nucléaire externe est bien développée, sauf dans les zones ventrale et temporo-ventrale. La couche plexiforme externe est relativement épaisse. A son niveau inférieur, le chaînon nucléaire constitué par les cellules horizontales allongées est parfaitement visible. Dans la couche nucléaire interne, le nombre de cellules bipolaires, horizontales et amacrines est beaucoup plus grand dans les zones ventrale et temporo-ventrale. Les amacrines se distinguent des bipolaires en ce qu'elles sont plus grosses et de coloration plus pâle, et qu'elles se situent à la limite inférieure de la nucléaire interne.

La couche ganglionnaire est particulièrement développée dans la zone ventrale d'abord, où l'on compte un nombre maximum de cellules ganglionnaires, et aussi dans la zone temporo-ventrale. Partout ailleurs, ces cellules sont faiblement représentées. La convergence calculée des éléments rétiniens, i.e., le rapport numérique cellules visuelles/ganglionnaires, fut estimée à 8 dans la zone ventrale, et à 1987 dans le fundus dorsal.

2. *CLUPEA HARENGUS* (FIG. 5, 6, 35, 36)

La couche visuelle présente un développement analogue à celui de l'espèce précédente. Les cônes y sont nombreux, mais il existe de grandes variations numériques d'une zone à l'autre (Fig. 1B). Les cônes sont simples ou doubles symétriques. Sauf dans la région temporo-ventrale où l'on trouve environ deux fois plus de cônes doubles que de simples, et dans la région temporale où les simples représentent le quart des effectifs, les cônes simples sont généralement absents ou très rares. L'area retinae (maximum de cônes) est temporo-ventrale (Fig. 36), et non ventrale comme celle du gaspareau. Verheijen (1959) a aussi décrit une area retinae chez le hareng, mais sa localisation (ventrale, à proximité du nerf optique) ne semble pas reposer sur un examen complet de la rétine.

La disposition spatiale des cônes telle qu'observée en coupes tangentielles s'apparente à celle du gaspareau. Temporalement et temporo-ventralement, la mosaïque est du type B de la Fig. 2 (Fig. 36). Dans la région naso-dorsale, nous observons le curieux arrangement G déjà décrit chez le gaspareau. Dans toutes les autres zones rétiniennes, la mosaïque comprend simplement des cônes doubles disposés en rangées parallèles, avec parfois des cônes simples occasionnels (Fig. 35). Engström (1963b) a déjà décrit la même disposition des mosaïques B et F chez le hareng, mais il n'a pas détaillé leur distribution dans la rétine.

Les bâtonnets sont particulièrement abondants. Toutefois ils sont relativement peu nombreux dans l'area retinae (Tableau 2). Les réponses photomécaniques de ces cellules visuelles existent chez le hareng et sont bien développées (Blaxter et Jones, 1967).

Au début de la nucléaire interne, les cellules horizontales sont souvent visibles, mais n'ont pas atteint un développement comparable à celui du gaspareau. La même observation s'applique aux cellules bipolaires et amacrines. Ce développement mitigé des éléments nerveux est plus évident dans les zones avantagées, si on compare avec les données d'*Alosa* (Tableau 2). La couche ganglionnaire présente des variations notables dans le nombre de cellules d'une région à l'autre. La zone temporo-ventrale et le fundus temporal sont les régions les plus favorisées. La convergence ou sommation fut estimée à 31 dans la région temporo-ventrale et à 561 dans la région dorsale.

3. *MALLOTUS VILLOSUS* (FIG. 7, 8, 37)

La couche visuelle ne possède que des cônes doubles, la plupart étant du type symétrique. Un nombre maximum de cônes est observé dans la région ventrale ou area retinae. La disposition spatiale des cônes est grandement simplifiée par le fait qu'ils sont monotypiques. Ils sont arrangés en séries parallèles F (Fig. 37), plus ou moins désintégrées au niveau du fundus.

Les bâtonnets sont nombreux, mais n'atteignent pas les densités estimées chez les Clupeidae. La région ventrale, dite area retinae, possède moins de bâtonnets que les autres zones, mais la différence n'est pas énorme. La couche nucléaire externe est composée des noyaux des cellules visuelles disposés en étages compacts. La nucléaire interne comprend des étages touffus de cellules horizontales, bipolaires et amacrines dans les zones spécialisées, telles les régions ventrale et temporale. Dans la région ventrale, le développement relatif des cellules horizontales et amacrines est unique et remarquable. Au niveau du fundus, les bipolaires sont clairsemées.

Les cellules ganglionnaires varient en abondance dans la rétine, formant deux couches cellulaires compactes en région ventrale, mais une seule couche

TABLEAU 2. Nombre de cellules rétiniennes pour une superficie donnée (0.04 mm^2) chez les Clupéiformes étudiés. S, D, T, Hor., Bip., Ama. signifient respectivement cônes simples, doubles, triples, cellules horizontales, bipolaires et amacrines.

Espèces	Zone rétinienne	Cônes			Bâtonnets	Hor.	Bip.	Ama.	Cellules ganglionnaires
		S	D	T					
Alosa pseudoharengus	Ventrale	258	525	–	1,976	225	2828	676	336
	Fundus dorsal	4	63	–	31,728	25	252	46	16
	Nasale	6	134	–	20,024	49	783	81	64
	Temporo-ventrale	109	302	–	10,765	81	2204	256	169
	Naso-dorsale	2	91	–	29,776	36	408	49	36
Clupea harengus	Ventrale	23	199	–	12,210	?	584	36	49
	Fundus temporal	36	345	–	19,265	81	708	94	100
	Nasale	–	120	–	30,068	25	871	64	36
	Temporo-ventrale	262	570	–	6,332	144	1294	324	225
	Dorsale	3	102	–	13,920	?	409	36	25
Mallotus villosus	Ventrale	–	655	–	6,447	324	756	570	354
	Dorsale	–	420	–	9,700	64	677	85	273
	Nasale	–	317	–	7,461	64	298	80	36
Osmerus mordax	Temporo-ventrale	338	567	–	8,017	180	1019	461	348
	Temporo-dorsale	72	228	–	9,413	81	686	256	64

de noyaux clairsemés au fundus. La convergence fut estimée à 20 ventralement et à 445 au fundus.

4. *OSMERUS MORDAX* (FIG. 38, 39)

Au niveau de la couche visuelle, les cônes sont bien représentés, et nous pouvons distinguer des cônes simples et doubles symétriques. Quelques éléments asymétriques, quant au diamètre, sont visibles. Les deux types de cônes abondent dans la région temporo-ventrale, mais les doubles dominent. D'après les coupes tangentielles, deux mosaïques sont observées: rangées parallèles alternantes de cônes simples et doubles (type E, Fig. 2) et rangées parallèles de cônes doubles (type F) avec cônes simples occasionnels. La mosaïque E est trouvée dans la région temporo-ventrale, zone de l'area retinae (Fig. 39).

Les bâtonnets présentent les mêmes caractéristiques que ceux de l'espèce précédente. La nucléaire interne est remarquablement développée. De même que chez le capelan, les cellules horizontales et amacrines sont relativement très abondantes dans l'area retinae. Les cellules bipolaires sont très nombreuses, et les ganglionnaires sont aussi bien représentées, surtout temporo-ventralement. La convergence fut estimée à 25 dans la région temporo-ventrale.

5. *TAUTOGOLABRUS ADSPERSUS* (FIG. 9, 10, 41, 42)

La couche des cellules visuelles est très bien développée dans toute la superficie rétinienne. Les cônes y sont très nombreux partout (Fig. 1C). Trois types de cônes peuvent être discernés (Fig. 3B): les cônes doubles symétriques, les cônes simples nains et les cônes simples géants. D'une facon générale, dans les zones spécialisées, il y a autant de cônes doubles que de cônes simples, et parmi ces derniers, les nains sont aussi nombreux que les géants. Dans les régions moins spécialisées, les cônes doubles dominent. Chez cette espèce,

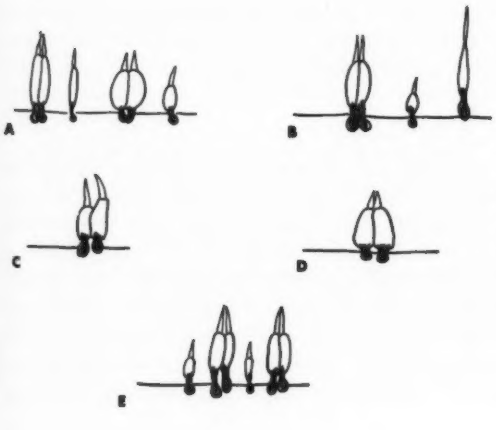


FIG. 3. Représentation schématique des cônes vus en coupe transversale chez quelques téléostéens étudiés. A, *Alosa*; B, *Tautogolabrus*; C, *Lycodes*; D, *Cyclopterus*; E, *Limanda*.

il est difficile de circonscrire topographiquement une area retinae, car il n'y a pas de forte spécialisation différentielle comme celle des Clupéiformes. Néammoins, un faible maximum de cônes est trouvé dans le fundus temporal.

L'observation des coupes tangentielles nous permet de reconnaître trois types de mosaïques à cônes inégalement distribués dans la rétine. Dans plusieurs zones plus spécialisées (ventrale, fundus ventral, naso-dorsale, nasale), la mosaïque est faite de cônes doubles constituant un carré avec cône simple central (= cône simple géant) et cônes simples accessoires (= cônes simples nains). Ce type A est représenté dans la Fig. 2 (Fig. 42). Les cônes accessoires ne sont pas toujours visibles, à cause de leur petite taille. Il s'agit d'atteindre le bon niveau dans la couche rétinienne. Certaines zones (fundus) ont perdu presque tous leurs cônes accessoires, et ont ainsi une mosaïque B. D'autres (dorsale, temporale, fundus temporal) ont vu leurs cônes doubles devenir parallèles (type E), avec alternance des cônes simples nains et géants.

Les bâtonnets sont plus nombreux que les cônes, mais leur abondance relative est passablement inférieure à celle observée chez les autres espèces. La distribution de leur densité dans les différentes zones rétiniennes ne semble pas suivre un arrangement précis. La couche nucléaire externe est peu développée, et est composée le plus souvent d'une ou deux couches de noyaux à bâtonnets plus ou moins compactes. Dans certaines régions (dorsale, naso-dorsale et autres), une dentelure nucléaire s'est constituée plus bas, au niveau de la plexiforme externe et au voisinage des cellules horizontales. Il est plausible que ce soit une seconde couche de cellules horizontales. Un arrangement analogue semble avoir été aperçu chez la sole par Engström et Ahlbert (1963) qui le décrivent comme un étage de noyaux à bâtonnets.

La région du fundus temporal possède au moins deux fois plus de cellules bipolaires que partout ailleurs dans la rétine, et son complément de cellules amacrines est important. Il reste que les bipolaires sont présentes en grand nombre sur toute la rétine, sauf au fundus. Également, le fundus temporal domine très fortement en ce qui a trait à l'abondance des cellules ganglionnaires. Ici encore, les autres régions sont néanmoins bien pourvues, sauf le fundus même. La convergence fut estimée à 20 dans le fundus temporal, et à 120 dans le fundus central (proximité du nerf optique).

6. *EUMESOGRAMMUS PRAECISUS* (FIG. 11, 40).

La couche visuelle comporte un nombre relativement modeste de cellules photosensorielles. Les cônes sont simples et doubles symétriques, ces derniers étant plus nombreux (Tableau 6). Les cônes simples sont représentés au maximum dans la région temporale, ou area retinae, où ils sont deux fois moins nombreux que les doubles. La disposition spatiale des cônes est passablement variable. Dans les régions temporale, temporo-dorsale, temporo-ventrale et ventrale, les cônes doubles forment un carré à cône simple central du type B. Dans la région dorsale cependant (Fig. 40), l'orientation du grand axe des cônes doubles change à 45° environ, et nous obtenons ainsi le type

C. Au niveau du fundus, l'orientation des cônes est semblable, mais les cônes simples sont rares ou absents (type D). Enfin, nasalement, la mosaïque est nettement du type F.

Les bâtonnets sont nombreux relativement à l'abondance des cônes, mais leurs densités absolues se comparent à celles de l'espèce précédente. La couche nucléaire externe est très mince, et les noyaux qu'elle comporte sont disposés en couches compactes. La nucléaire interne, par contre, a connu un développement remarquable, avec une abondance particulière de cellules bipolaires, surtout temporalement. Les cellules amacrines sont relativement nombreuses et très nettement distinctes des bipolaires. La couche ganglionnaire a atteint un très haut niveau de développement, et en ce sens la région temporale contraste fortement avec les zones avoisinantes. La convergence fut estimée à 7 temporalement et à 31 au fundus.

7. *LYCODES LAVALEI* (FIG. 12, 43).

La couche visuelle est faiblement développée. Les cônes sont relativement peu nombreux. Les cônes doubles, symétriques ou asymétriques (Fig. 3C), sont fortement majoritaires, même dans l'area retinae où la proportion des cônes simples est la plus élevée (zone temporo-dorsale). Un très petit nombre de cônes triples du type triangulaire est enregistré dans quelques zones. La disposition spatiale des cônes est grandement simplifiée. Dans les régions temporo-dorsale et temporo-ventrale, il s'agit d'une mosaïque F avec cônes simples occasionnels. Parfois les rangées parallèles de cônes doubles sont partiellement désintégrées. Dans d'autres zones (ventrale, nasale, fundus, etc.), il s'agit sans équivoque d'une mosaïque désintégrée de type H (Fig. 43).

Les bâtonnets sont fort nombreux, et constituent les éléments dominants de la couche visuelle. La couche nucléaire externe comprend un grand nombre de noyaux serrés les uns contre les autres. La nucléaire interne est peu développée et, sauf pour la zone temporo-dorsale, est relativement pauvre en cellules bipolaires. Les cellules amacrines et horizontales sont si peu nombreuses qu'on ne peut les compter bien souvent (Tableau 3). La couche ganglionnaire est très peu développée dans la plupart des zones rétiniennes. Même dans l'area retinae, les cellules ganglionnaires sont fort mal représentées. La convergence est de 392 temporo-dorsalement à 2240 nasalement.

8. *LYCODES RETICULATUS* (FIG. 13, 44–46)

La couche visuelle a la même allure générale que celle de *L. lavalei*. Toutefois, des divergences peuvent être signalées entre le jeune lycode et l'adulte (Tableau 3). Bien que la zone à maximum de cônes soit la même, temporo-dorsale, chez les deux individus, la densité des cônes et bâtonnets est beaucoup plus élevée chez le jeune. De plus, les cônes triples du type triangulaire, rencontrés chez l'adulte, sont complètement absents chez le jeune examiné. La disposition spatiale des cônes ne diffère pas de celle de l'espèce précédente, à cette exception près qu'une tendance plus prononcée vers la désintégration

TABLEAU 3. Nombre de cellules rétiniennes pour une superficie donnée (0.04 mm^2) chez les lycodes étudiés.[a]

Espèces	Zone rétinienne	Cônes			Bâtonnets	Hor.	Bip.	Ama.	Cellules ganglionnaires
		S	D	T					
Lycodes lavalei	Ventrale	4	52	–	9,009	?	261	?	9
	Temporo-dorsale	15	94	2	14,064	25	442	?	36
	Nasale	2	31	2	6,687	?	63	?	3
L. reticulatus (725 mm)	Ventrale	–	29	–	9,399	?	502	19	4
	Temporo-dorsale	5	74	1	10,418	?	343	16	25
	Nasale	3	61	–	5,969	?	334	4	4
	Fundus	1	25	–	7,533	?	143	?	9
L. reticulatus (290 mm)	Temporo-ventrale	7	77	–	7,752	36	765	16	16
	Temporo-dorsale	9	175	–	27,028	100	684	81	121
	Fundus	9	125	–	13,157	9	361	4	16
L. turneri	Nasale	7	91	2	11,373	16	632	10	36
	Temporo-dorsale	38	127	–	9,348	36	803	81	144
	Fundus	9	54	2	12,165	?	219	?	9
L. vahlii	Ventrale	5	61	–	10,315	?	510	9	25
	Temporo-ventrale	7	104	–	9,417	16	612	25	36
	Temporale	9	212	–	14,901	16	894	49	100

[a] Voir Tableau 2 pour l'explication des abréviations.

des mosaïques est constatée. Cette tendance est nette chez l'adulte (Fig. 44) où même l'area retinae montre une mosaïque bien désintégrée.

Les cellules bipolaires, et à un degré moindre, les cellules horizontales et amacrines, sont plus nombreuses chez le jeune lycode. Le même phénomène se répète chez les ganglionnaires. La convergence est de 419 chez l'adulte, et de 224 chez le jeune, pour la zone temporo-dorsale.

9. *Lycodes turneri* (Fig. 14, 15)

L'area retinae est temporo-dorsale. A cet endroit le nombre de cônes simples est relativement élevé. Par contre, et cette situation est nouvelle chez les lycodes, le nombre de bâtonnets est faible à cet endroit. Les cônes triples sont présents dans certaines zones, et même de rares cônes quadruples dans quelques régions (temporale, temporo-ventrale, fundus). La mosaïque des cônes est désintégrée totalement, sauf dans les zones temporo-dorsale, ventrale et dorsale où l'on observe des rangées parallèles plus ou moins ordonnées.

Le nombre de cellules bipolaires est relativement élevé, surtout dans l'area retinae, et parallèlement chez les cellules ganglionnaires. La convergence s'estime à 66 dans la région temporo-dorsale.

10. *Lycodes vahlii* (Fig. 47, 48)

Contrairement aux lycodes précédents, l'area retinae est temporale (Fig. 47), avec un nombre maximum de cônes dépassant celui de tous les autres lycodes examinés. Aucun cône triple ni quadruple ne fut observé. Les couches internes sont mieux développées que chez tout autre lycode. Ceci s'adresse particulièrement aux cellules bipolaires, dont le nombre est supérieur temporalement. La convergence est de 151 temporalement et de 2168 au fundus.

11. *Lycodes* sp. (Fig. 16, 17)

L'area retinae relative est temporale. Les cônes triples, du type triangulaire, sont peu nombreux mais présents partout. Aucun cône quadruple n'a été observé. Seules les zones temporale et temporo-dorsale possèdent une mosaïque non désintégrée du type F avec cônes simples et triples occasionnels. Les couches internes montrent un maigre développement analogue à celui des autres lycodes. La convergence est de 344 dans la zone temporale.

12. *Myoxocephalus octodecemspinosus* (Fig. 18, 50, 51)

La couche visuelle est bien développée. Les cônes y sont bien représentés et sont de deux sortes: simples et doubles symétriques, ces derniers étant de beaucoup les plus nombreux. Dans certaines zones (temporo-dorsale, fundus), les cônes simples représentent environ le tiers des effectifs. L'area retinae est temporale.

La disposition spatiale des cônes présente de grandes variations. La mosaïque des zones ventrale et temporo-ventrale appartient nettement au type B précédemment décrit. Le fundus (Fig. 51) et la zone nasale ont plutôt une mosaïque du type C, avec une orientation du grand axe des cônes doubles à 45° plutôt qu'à 90° comme le type B. La région temporo-dorsale apparaît transitionnelle entre B et C. Des rangées parallèles de cônes doubles (type F) sont observées dans les zones dorsale et temporale (Fig. 50), tandis que les nombreux et petits cônes simples sont trouvés à un niveau inférieur de la coupe.

Les bâtonnets sont très nombreux, et particulièrement au niveau du fundus. La couche nucléaire interne est plus ou moins développée selon les régions. Dans les zones ventrale et temporale, les cellules bipolaires sont remarquablement représentées. L'abondance relative des cellules amacrines est élevée, surtout temporalement. Les horizontales constituent une couche mal définie au-dessus des bipolaires. La couche ganglionnaire est en général bien développée dans quelques zones seulement, soient les zones temporale et temporo-ventrale. La convergence est de 29 temporalement et de 5425 au fundus.

13. *MYOXOCEPHALUS SCORPIUS* (Fig. 19, 52, 53)

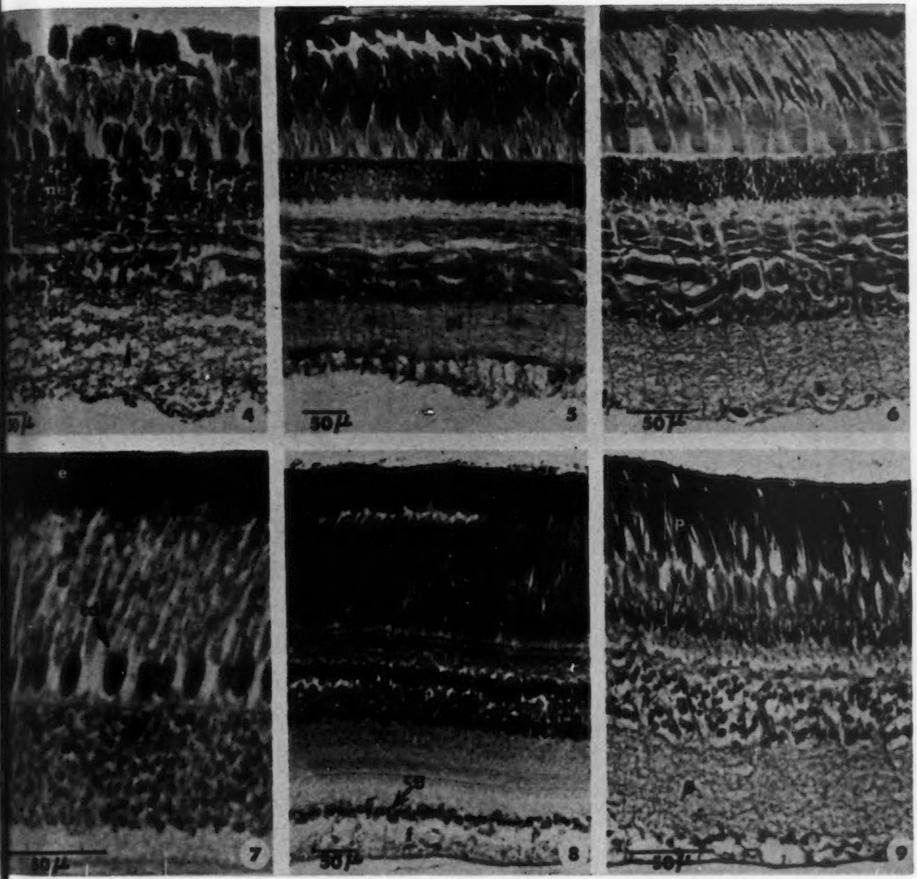
Dans la couche visuelle, les cônes y sont aussi bien représentés que ceux de l'espèce précédente. Ils sont généralement de deux types: simples et doubles symétriques, ces derniers étant majoritaires. Toutefois, des cônes triples du type triangulaire et des cônes quadruples sont observés dans la région ventrale, dans une aire de désintégration très locale. Dans la région temporale, ou area retinae, les cônes simples constituent près de la moitié du stock des cônes doubles.

La disposition spatiale des cônes diffère légèrement de celle de l'espèce parente. Une mosaïque régulière du type B est signalée pour les zones dorsale, nasale, temporo-ventrale (Fig. 52) et temporo-dorsale; la même mosaïque montre des signes de désintégration au fundus. Dans l'area retinae (temporale), la mosaïque s'apparente au type C. Une aire désintégrée de type H est localisée dans la région ventrale (Fig. 53).

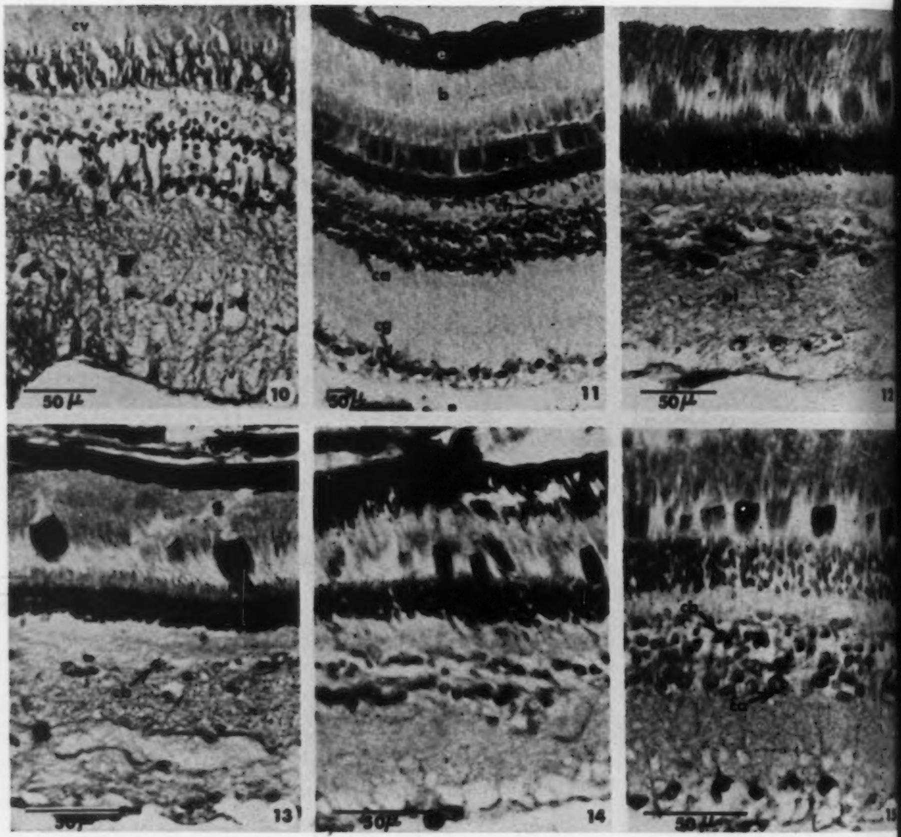
Les bâtonnets sont bien développés; leur densité maximum est atteinte en zone temporale. La couche nucléaire interne est bien représentée en éléments bipolaires, surtout temporalement, mais moins bien que celle de l'espèce parente. La couche ganglionnaire est développée essentiellement de la même facon que celle de *Myoxocephalus octodecemspinosus*. La convergence est de 40 temporalement et 587 au fundus.

14. *TRIGLOPS MURRAYI* (FIG. 20, 21, 49)

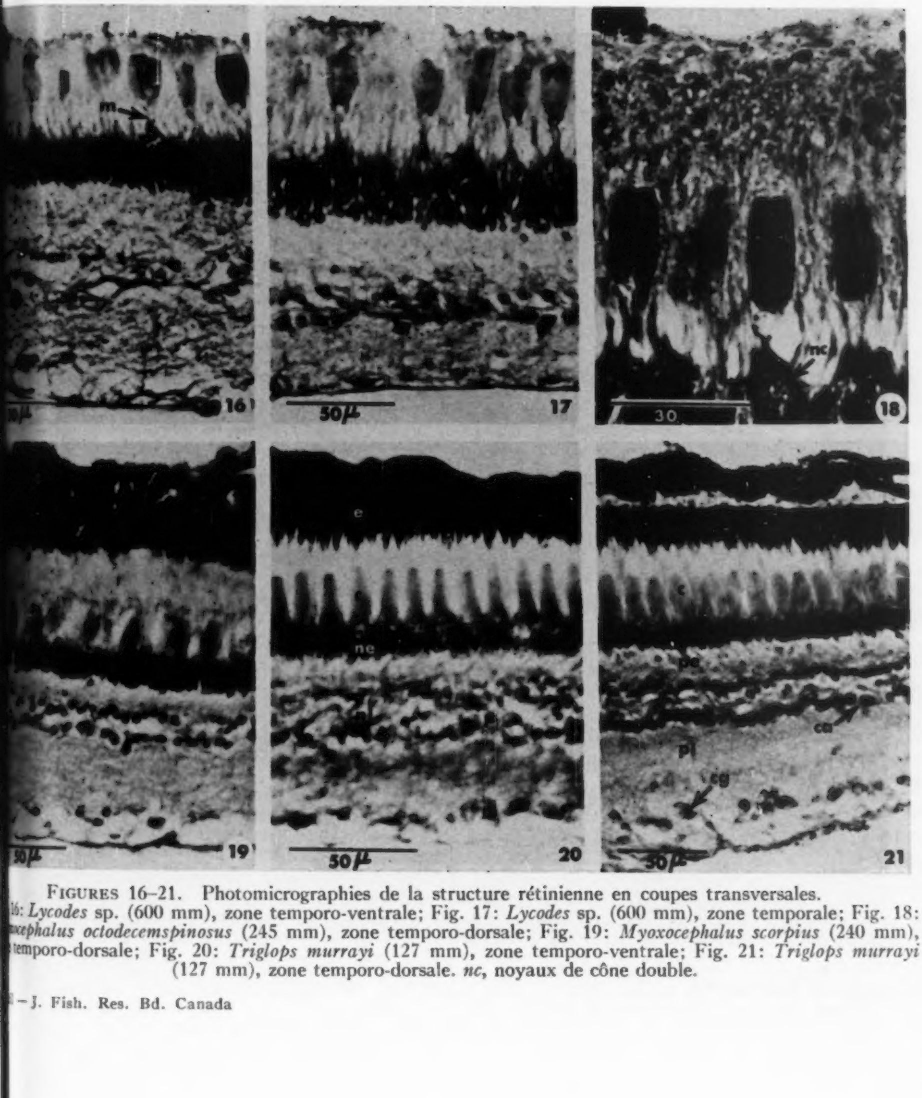
La couche visuelle est particulièrement bien fournie en éléments photosensoriels. Les cônes sont très nombreux, comparativement aux autres Cottidae étudiés (Tableau 4). Seuls les cônes simples et doubles symétriques sont représentés, ces derniers étant majoritaires. La région temporo-ventrale, zone à maximum de cônes, contient deux fois plus de cônes doubles que de simples. La disposition spatiale est simplifiée chez cette espèce. Il s'agit tou-



Figures 4–9. Photomicrographies de la structure rétinienne en coupes transversales. 4: *Alosa pseudoharengus* (340 mm), zone naso-dorsale; Fig. 5: *Clupea harengus* (325 mm), zone du fundus tral; Fig. 6: *Clupea harengus* (350 mm), zone naso-dorsale; Fig. 7: *Mallotus villosus* (160 mm), zone du fundus; 8: *Mallotus villosus* (160 mm), zone ventrale; Fig. 9: *Tautogolabrus adspersus* (255 mm), zone temporale. âtonnets; *c*, cônes; *cd*, cône double; *cg*, cellules ganglionnaires; *e*, épithélium pigmenté; *f*, couche des fibres euses; *le*, limitans externe; *m*, myoïde de cône; *ne*, couche nucléaire externe; *ni*, couche nucléaire interne; *p*, pigment épithélial; *pe*, couche plexiforme externe; *pi*, couche plexiforme interne.



Figures 10–15. Photomicrographies de la structure rétinienne en coupes transversales. Fig. 10: *Tautogolabrus adspersus* (255 mm), zone du fundus dorsal; Fig. 11: *Eumesogrammus praecisus* (1 mm), zone temporale; Fig. 12: *Lycodes lavalei* (640 mm), zone dorsale; Fig. 13: *Lycodes reticulatus* (725 m zone du fundus; Fig. 14: *Lycodes turneri* (245 mm), zone temporale périphérique; Fig. 15: *Lycodes turn* (245 mm), zone temporo-dorsale. *ca*, cellules amacrines; *cb*, cellules bipolaires; *ch*, cellules horizontal *cv*, couche visuelle.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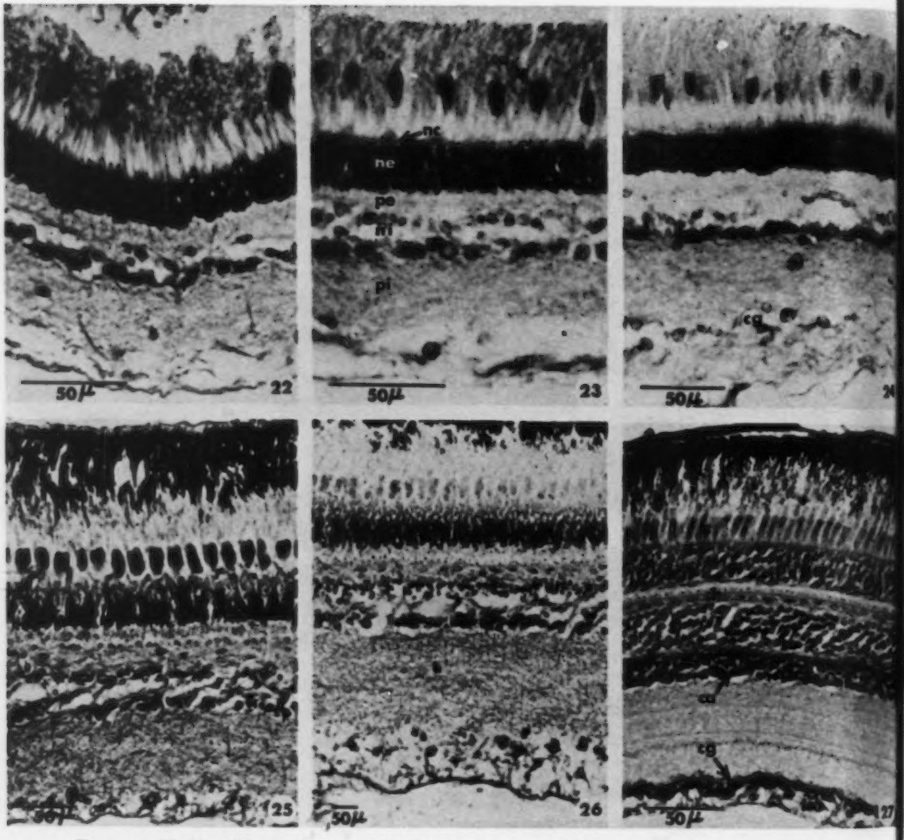
FIGURES 16–21. Photomicrographies de la structure rétinienne en coupes transversales. 16: *Lycodes* sp. (600 mm), zone temporo-ventrale; Fig. 17: *Lycodes* sp. (600 mm), zone temporale; Fig. 18: *cephalus octodecemspinosus* (245 mm), zone temporo-dorsale; Fig. 19: *Myoxocephalus scorpius* (240 mm), temporo-dorsale; Fig. 20: *Triglops murrayi* (127 mm), zone temporo-ventrale; Fig. 21: *Triglops murrayi* (127 mm), zone temporo-dorsale. *nc*, noyaux de cône double.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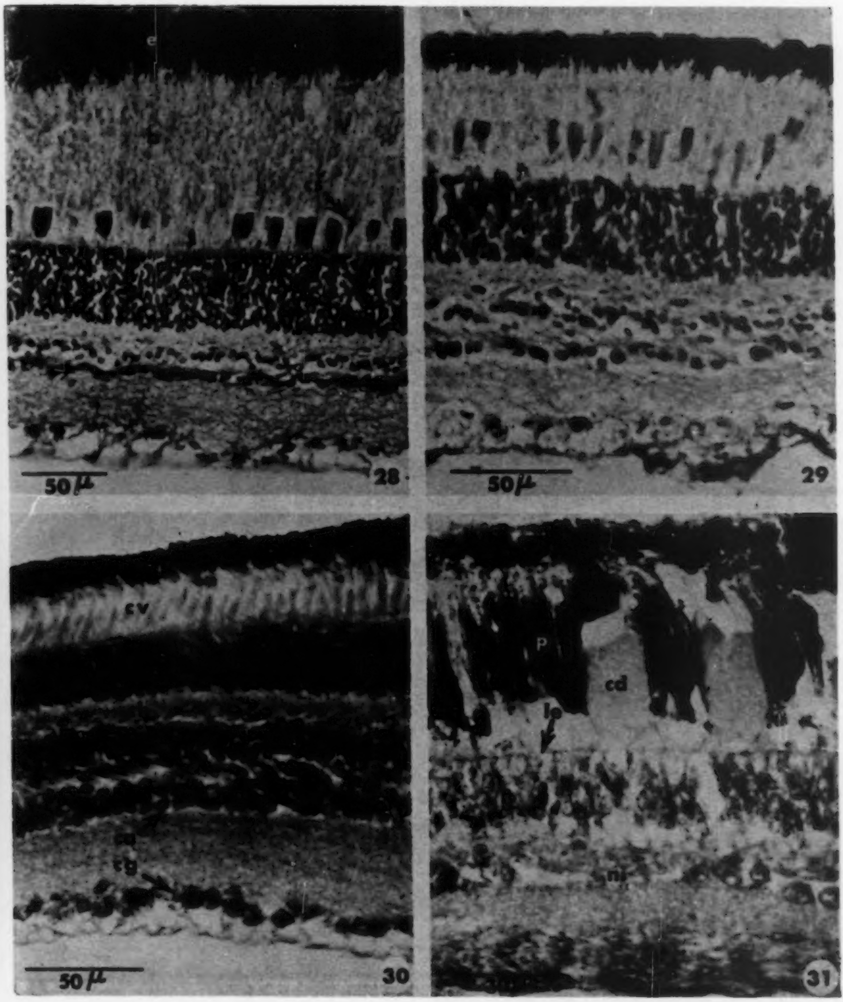
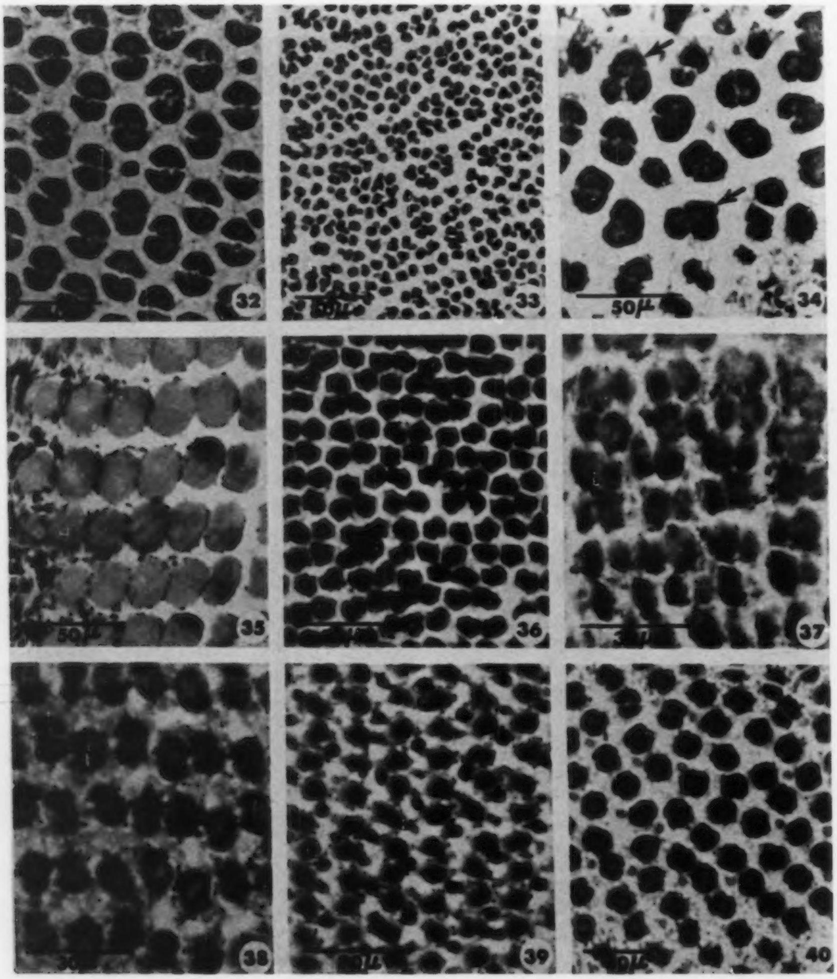
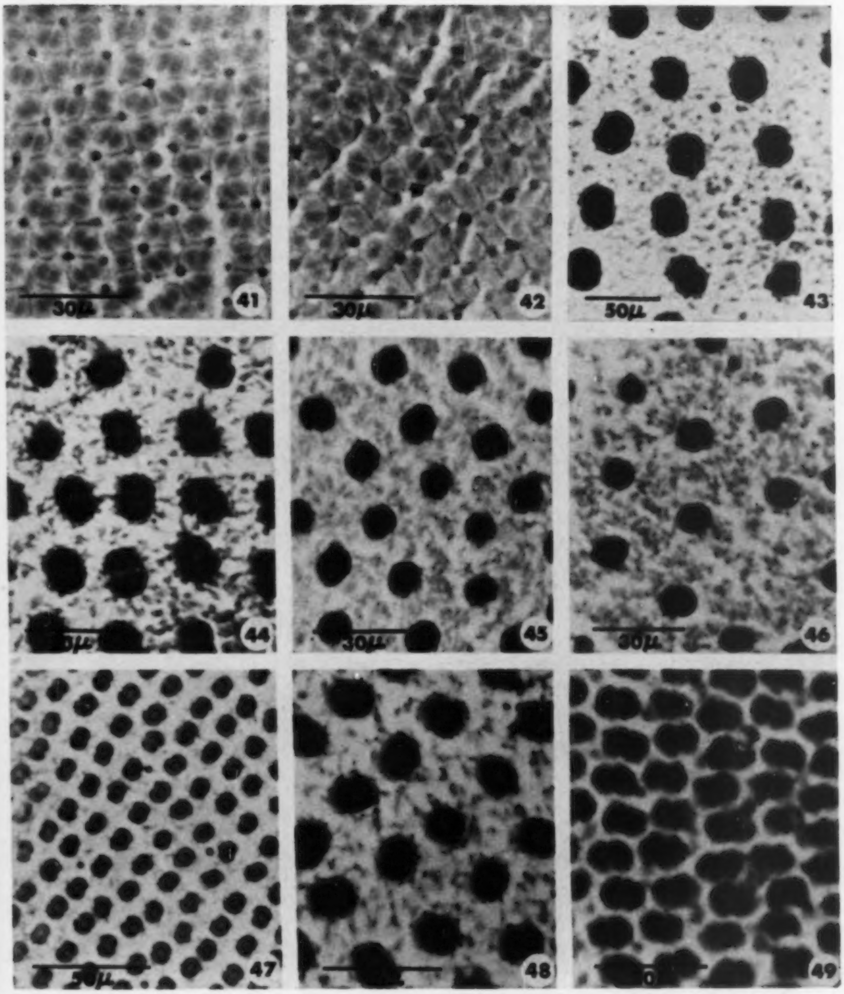
FIGURES 22–27. Photomicrographies de la structure rétinienne en coupes transversales. Fig. 22: *Agonus decagonus* (203 mm), zone temporo-ventrale; Fig. 23: *Aspidophoroides monopterygius* (mm), zone dorsale; Fig. 24: *Aspidophoroides monopterygius* (210 mm), zone du fundus; Fig. 25: *Cyclopte* *lumpus* (290 mm), zone dorsale; Fig. 26: *Cyclopterus lumpus* (290 mm), zone temporo-ventrale; Fig. *Glyptocephalus cynoglossus* (130 mm), zone ventrale. *nc*, noyau de cône.



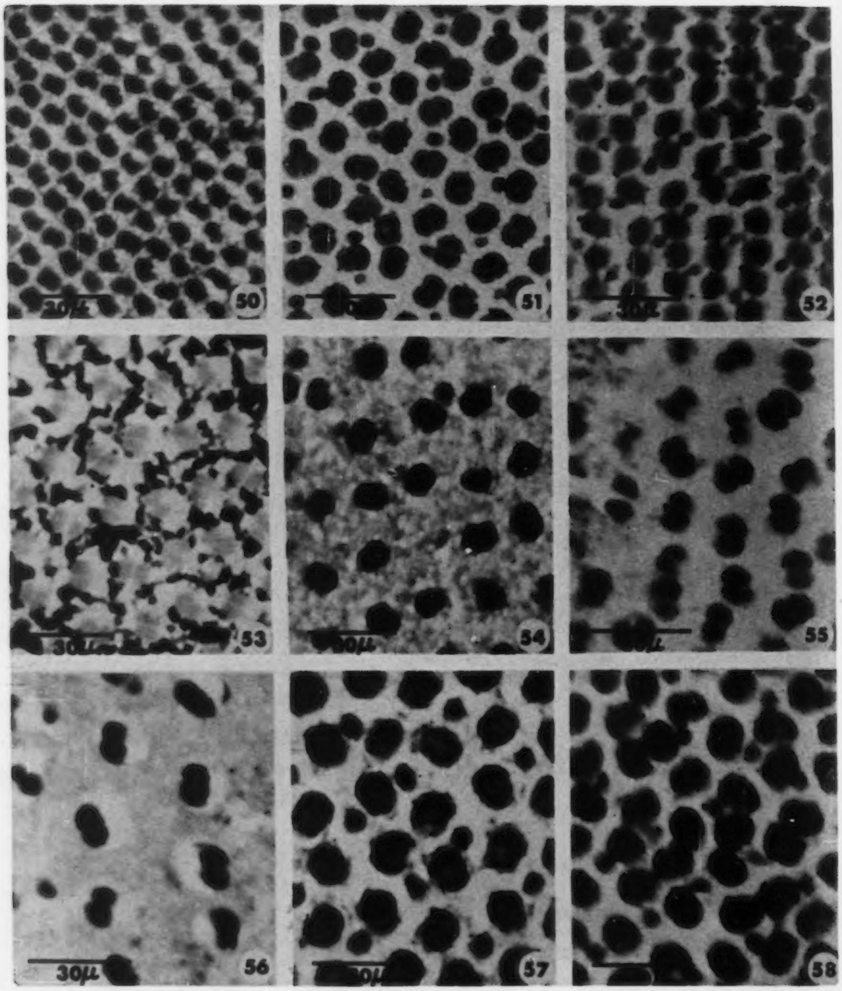
FIGURES 28–31. Photomicrographies de la structure rétinienne en coupes transversales. Fig. 28: *Glyptocephalus cynoglossus* (435 mm), zone temporale; Fig. 29: *Limanda ferruginea* (143 mm), zone nasale; Fig. 30: *Limanda ferruginea* (143 mm), zone ventrale périphérique; Fig. 31: *Lophius americanus* (690 mm), zone du fundus. *cs*, cône simple.



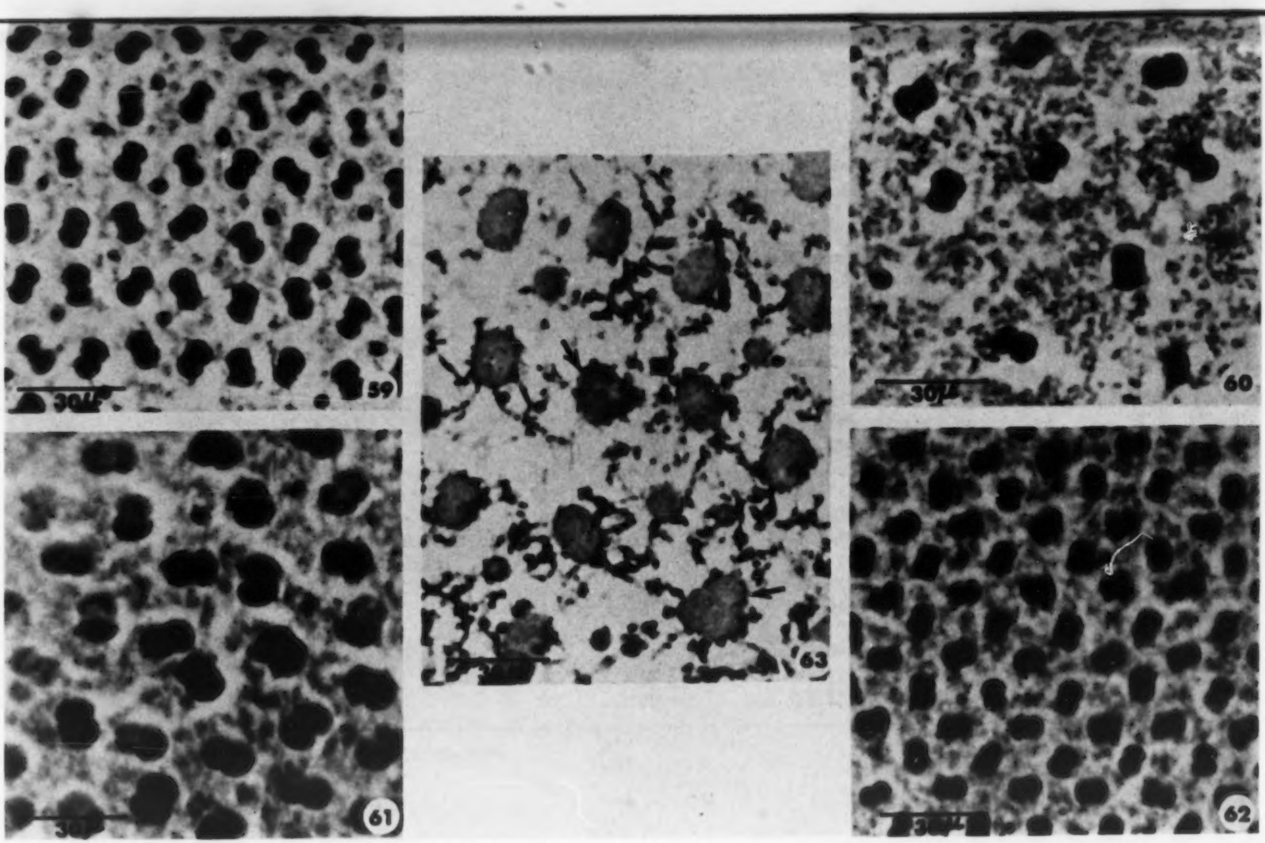
FIGURES 32–40. Photomicrographies des cellules visuelles en coupes tangentielles. Fig. 32: *Alosa pseudoharengus* (340 mm), zone du fundus dorsal; Fig. 33: *Alosa pseudoharengus* (340 mm), zone ventrale ou région d'acuité; Fig. 34: *Alosa pseudoharengus* (340 mm), zone désintégrée du fundus; Fig. 35: *Clupea harengus* (350 mm), zone dorsale; Fig. 36: *Clupea harengus* (350 mm), proximité de la zone temporo-ventrale ou zone d'acuité; Fig. 37: *Mallotus villosus* (165 mm), zone temporale; Fig. 38: *Osmerus mordax* (175 mm), zone temporo-dorsale; Fig. 39: *Osmerus mordax* (175 mm), zone temporo-ventrale; Fig. 40: *Eumesogrammus praecisus* (138 mm), zone dorsale. Les flèches indiquent des cônes triples.



FIGURES 41–49. Photomicrographies des cellules visuelles en coupes tangentielles. Fig. 41: *Tautogolabrus adspersus* (255 mm), zone temporo-dorsale; Fig. 42: *Tautogolabrus adspersus* (255 mm), zone ventrale; Fig. 43: *Lycodes lavalei* (640 mm), zone dorsale; Fig. 44: *Lycodes reticulatus* (725 mm), zone temporo-dorsale ou région d'acuité; Fig. 45: *Lycodes reticulatus* (290 mm), zone nasale; Fig. 46: *Lycodes reticulatus* (290 mm), zone temporo-ventrale; Fig. 47: *Lycodes vahlii* (226 mm), zone temporale ou région d'acuité; Fig. 48: *Lycodes vahlii* (226 mm), zone du fundus; Fig. 49: *Triglops murrayi* (127 mm), zone nasale.



FIGURES 50–58. Photomicrographies des cellules visuelles en coupes tangentielles. Fig. 50: *Myoxocephalus octodecemspinosus* (245 mm), zone temporale ou région d'acuité; Fig. 51: *Myoxocephalus octodecemspinosus* (245 mm), zone du fundus; Fig. 52: *Myoxocephalus scorpius* (240 mm), zone temporo-ventrale; Fig. 53: *Myoxocephalus scorpius* (240 mm), zone ventrale avec le pigment épithélial entourant les cônes; Fig. 54: *Agonus decagonus* (203 mm), zone temporo-dorsale; Fig. 55: *Aspidophoroides monopterygius* (187 mm), zone nasale; Fig. 56: *Aspidophoroides monopterygius* (187 mm), zone ventrale; Fig. 57: *Cyclopterus lumpus* (290 mm), zone dorsale; Fig. 58: *Cyclopterus lumpus* (290 mm), zone temporo-ventrale.



Figures 59–63. Photomicrographies des cellules visuelles en coupes tangentielles.
Fig. 59: *Glyptocephalus cynoglossus* (435 mm), zone du fundus ventral ou région d'acuité; Fig. 60: *Glyptocephalus cynoglossus* (435 mm), zone temporale; Fig. 61: *Limanda ferruginea* (290 mm), zone du fundus; Fig. 62: *Limanda ferruginea* (290 mm), zone ventrale; Fig. 63: *Lophius americanus* (690 mm), zone du fundus temporal. Les flèches indiquent des cônes triples.

TABLEAU 4. Nombre de cellules rétiniennes pour une superficie donnée (0.04 mm^2) chez les Perciformes du sous-ordre Cottoidei.[a]

Espèces	Zone rétinienne	Cônes			Bâtonnets	Hor.	Bip.	Ama.	Cellules ganglionnaires
		S	D	T					
Myoxocephalus octodecemspinosus	Temporale	123	372	–	13,029	121	1738	440	460
	Dorsale	?	228	–	13,501	?	911	182	121
	Fundus	91	179	–	24,143	?	1061	195	45
M. scorpius	Temporale	154	350	–	15,358	81	1069	734	389
	Dorsale	75	163	–	6,716	?	765	?	49
	Fundus	39	91	–	9,274	9	462	?	16
Triglops murrayi	Temporo-ventrale	295	609	–	6,638	121	1272	136	249
	Nasale	131	316	–	8,213	36	696	45	225
	Fundus	43	100	–	16,036	49	652	36	36
Agonus decagonus	Temporo-ventrale	–	134	2	10,470	?	501	16	144
	Temporo-dorsale	–	124	1	10,424	?	461	16	16
Aspidophoroides monopterygius	Temporale	–	190	–	14,889	?	502	64	136
	Dorsale	25	81	–	10,644	?	709	25	230
	Fundus	14	41	–	11,175	?	587	25	100
Cyclopterus lumpus	Ventrale	161	335	–	8,692	169	953	81	64
	Nasale	52	123	–	10,424	36	543	36	16
	Fundus	95	192	–	7,228	36	865	25	81

[a] Voir Tableau 2 pour l'explication des abréviations.

jours du type C pour toutes les zones rétiniennes observées (Fig. 49) et il est à peine dissolu au niveau du fundus. Dans certaines régions où la proportion des cônes simples est plus faible (dorsale, temporo-dorsale, etc.), la mosaïque tend à s'assimiler au type D.

La couche nucléaire interne est relativement bien développée. Elle contient un grand nombre de cellules bipolaires dans la zone temporo-ventrale, mais la proportion de cellules horizontales et amacrines semble plutôt faible. La couche ganglionnaire est peu développée; les cellules ganglionnaires se constituent le plus souvent en une rangée unique d'éléments clairsemés. La convergence est de 30 du côté temporo-ventral, et de 449 au fundus.

15. *AGONUS DECAGONUS* (FIG. 22, 54)

La couche visuelle comporte un nombre relativement faible de cônes. Ceux-ci sont presque tous doubles, symétriques ou asymétriques en proportions variables. En coupe tangentielle, quelques éléments ressemblent à des cônes simples, mais il semble que ce soient plutôt des cônes doubles asymétriques dont les deux éléments ne répondent pas également à l'adaptation à l'obscurité. Ceci a été révélé par l'examen des coupes transversales. La disposition spatiale des cônes se réduit simplement à des rangées parallèles (Fig. 54) plus ou moins harmonieuses de cônes doubles dont le grand axe montre deux orientations alternantes (mosaïque D).

Les bâtonnets sont nombreux par rapport aux cônes. La couche nucléaire externe comprend deux ou trois rangées de noyaux à bâtonnets, lesquels noyaux sont relativement énormes. La nucléaire interne est peu développée. Les cellules bipolaires sont faiblement représentées, les horizontales ne sont pas clairement discernables, tandis que les amacrines sont fort réduites en nombre. La couche ganglionnaire, parallèlement, présente un développement mitigé temporo-ventralement, et très faible temporo-dorsalement. La convergence est de 73 dans la zone temporo-ventrale.

16. *ASPIDOPHOROIDES MONOPTERYGIUS* (FIG. 23, 24, 55, 56)

Dans la couche visuelle, les cônes sont simples ou doubles, ces derniers étant symétriques en majorité. Aucun cône triple n'a été observé. Les cônes simples sont proportionnellement peu abondants, et même absents en zones temporale et nasale. L'area retinae est temporale. La disposition spatiale des cônes est plus variable que celle de l'espèce précédente. Dorsalement et ventralement (Fig. 56), la mosaïque est du type C en raison de la présence des cônes simples. Avec le départ ou la diminution de ces cônes en zones temporale et temporo-ventrale, la mosaïque devient du type D. Nasalement (Fig. 55), le grand axe des cônes doubles se redresse, et nous obtenons le type F. Au fundus, la mosaïque C est partiellement désintégrée.

Les bâtonnets sont relativement nombreux chez cette espèce. La couche nucléaire interne est peu développée, comme l'indique le dénombrement des cellules bipolaires (Tableau 4). Le maximum de bipolaires enregistré n'est pas temporal, zone de l'area retinae à cônes doubles exclusifs, mais dorsal où l'on compte un certain nombre de cônes simples. Parallèlement à cette observation, le nombre maximum de ganglionnaires est localisé dorsalement. Les noyaux ganglionnaires sont de deux sortes en ce qui a trait à leur taille. La convergence est de 110 temporalement et de 46 dorsalement.

17. *CYCLOPTERUS LUMPUS* (FIG. 25, 26, 57, 58)

La couche visuelle est relativement bien développée, et les cellules visuelles la composant sont très abondantes. Les cônes y sont bien représentés, même dans les zones les moins spécialisées. Seuls les cônes simples et doubles symétriques ont été observés, ces derniers étant en général deux fois ou encore plus nombreux. L'area retinae est ventrale, mais elle est talonnée de près par la région temporo-ventrale (Fig. 58). La disposition spatiale des cônes comprend la mosaïque du type B pour les zones ventrale, temporo-ventrale (Fig. 58), temporale et temporo-dorsale; la mosaïque modifiée du type C se rencontre au fundus et dorsalement (Fig. 57). Le quadrilatère à cône simple central est partiellement désintégré du côté nasal.

Les bâtonnets sont numériquement bien représentés, bien que la couche nucléaire externe soit relativement étroite. Dans la nucléaire interne, les cellules bipolaires sont assez bien représentées dans toute les zones, et atteignent un maximum en zone temporo-ventrale. La couche ganglionnaire, par contre, est remarquablement faible, et ne comporte que quelques noyaux linéairement dispersés. La convergence est de 143 ventralement et de 91 au fundus.

18. *GLYPTOCEPHALUS CYNOGLOSSUS* (FIG. 27, 28, 59, 60)

La couche visuelle est très bien développée, et les cellules visuelles la composant sont très abondantes. Les cônes sont bien représentés, et sont simples et doubles symétriques. La proportion des cônes simples est toujours faible dans presque toutes les régions. La région du fundus ventral est celle qui comporte un maximum de cônes. La disposition spatiale des cônes réunit plusieurs conditions chez cette espèce. Au fundus ventral (Fig. 59), ou area retinae, et en zone temporale (Fig. 60), nous trouvons la mosaïque quadrilatère du type B. Dans les autres régions, la mosaïque est désintégrée à divers degrés, se rapprochant du type H, mais en tenant compte de l'absence des cônes triples.

Les bâtonnets peuvent être fort nombreux dans certaines zones rétiniennes, et même dans l'area retinae (Tableau 5). La couche nucléaire externe est bien développée et est composée de noyaux minuscules. La nucléaire interne a atteint un développement remarquable et, en ce sens, le fundus ventral (area) contraste fortement avec les zones avoisinantes. Les cellules bipolaires sont généralement nombreuses. Parallèlement, les cellules horizontales et amacrines forment deux couches bien structurées au fundus ventral ou ventralement (Fig. 27). La couche ganglionnaire est relativement bien développée au niveau du fundus ventral périphérique, mais elle devient rapidement pauvre dans les régions avoisinantes et temporalement (Fig. 28). La convergence est de 10 à l'area retinae et de 622 dans la zone temporo-dorsale.

TABLEAU 5. Nombre de cellules rétiniennes pour une superficie donnée (0.04 mm²) chez les pleuronectes étudiés.[a]

Espèces	Zone rétinienne	Cônes			Bâtonnets	Hor.	Bip.	Ama.	Cellules ganglionnaires
		S	D	T					
Glyptocephalus cynoglossus	Fundus ventral[b]	153	628	–	3,748	425	2329	1044	440
	Fundus ventral	16	58	–	10,807	225	419	225	100
	Temporo-ventrale	25	106	–	11,303	56	698	144	64
	Temporale	95	402	–	9,716	125	997	350	144
	Temporo-dorsale	30	76	–	15,463	10	515	?	25
Limanda ferruginea (290 mm)	Temporo-dorsale	325	668	–	9,571	289	1366	721	225
	Dorsale	229	468	–	8,963	121	1080	256	121
	Nasale	77	166	–	18,135	?	654	?	49
	Fundus	29	98	–	16,263	?	466	16	25
L. ferruginea (143 mm)	Dorsale	303	618	–	9,894	196	1227	381	324
	Temporo-dorsale	–	47	140	12,505	64	648	441	144
	Nasale	211	434	–	14,183	100	902	81	100
	Fundus	86	195	–	25,819	36	831	81	49

[a] Voir Tableau 2 pour l'explication des abréviations.
[b] A mi-chemin entre le véritable fundus ventral et la périphérie ventrale de la rétine.

TABLEAU 6. Nombre de cellules rétiniennes pour une superficie donnée (0.04 mm^2) chez diverses espèces étudiées.[a]

Espèces	Zone rétinienne	Cônes			Bâtonnets	Hor.	Bip.	Ama.	Cellules ganglionnaires
		S	D	T					
Tautogolabrus adspersus	Fundus temporal	554	629	–	5299	196	2984	1139	324
	Ventrale	474	475	–	3746	100	1294	121	100
	Naso-dorsale	533	504	–	2218	196	1393	793	144
	Fundus ventral	400	411	–	3863	81	1539	693	121
	Nasale	497	504	–	4752	81	1433	976	144
	Fundus	180	279	–	5429	36	811	64	49
Eumesogrammus praecisus	Temporale	141	272	–	5621	169	1141	787	784
	Temporo-dorsale	55	120	–	3641	64	924	528	400
	Nasale	6	77	–	2333	36	495	121	144
Lophius americanus	Temporo-dorsale	25	56	3	7242	?	149	?	9
	Ventrale	12	54	4	8642	16	201	4	16
	Fundus nasal	13	29	1	7733	?	81	9	4
	Fundus temporal	9	30	2	7091	?	?	?	?

[a] Voir Tableau 2 pour l'explication des abréviations.

19. *LIMANDA FERRUGINEA* (FIG. 29, 30, 61, 62)

La couche visuelle est très bien développée, comme celle de la plie grise. Les cônes y sont très nombreux, particulièrement en zone temporo-dorsale chez l'adulte (area retinae), et en zone dorsale chez le jeune (Tableau 5). La proportion de cônes simples est plus élevée que celle observée chez *G. cynoglossus*, représentant ici le tiers des effectifs totaux dans plusieurs régions rétiniennes. Assez curieusement, ils sont absents chez la jeune limande dans la zone temporo-dorsale, où l'on trouve une abondance unique et singulière de cônes triples du type triangulaire. Les cônes doubles sont généralement majoritaires, et peuvent être symétriques ou asymétriques (Fig. 3E).

La disposition spatiale des cônes est plus variable chez cette espèce que chez la plie grise. Chez l'adulte, un quadrilatère du type B est observé en zone ventrale (Fig. 62), et en zones temporo-ventrale et temporale; dans les régions temporo-dorsale, dorsale et nasale, le type C est plutôt trouvé. Au fundus (Fig. 61), la mosaïque est irrégulière et intermédiaire entre B et C. Chez la jeune limande, le type B est virtuellement absent, tandis que le quadrilatère à 45° est trouvé plus ou moins régulièrement dans la majorité des zones. Les exceptions comprennent la zone temporo-dorsale, qui est une aire de désintégration totale du type H, et la région du fundus, du type H mais sans cônes triples.

Les bâtonnets sont très abondants et peuvent atteindre des densités remarquablement élevées au niveau du fundus, surtout chez la jeune limande. Chez cette espèce comme chez la précédente, la longueur des bâtonnets peut être relativement très grande par rapport à celle des cônes, surtout dans les zones peu spécialisées.

D'une façon générale, les cellules bipolaires sont bien représentées, autant chez l'adulte que chez la jeune limande. L'abondance relative des cellules amacrines n'est remarquable que dans les régions rétiniennes spécialisées. La couche ganglionnaire est faiblement développée dans presque toutes les régions rétiniennes, sauf les areae retinae respectives du jeune et de l'adulte. A cet égard, les noyaux ganglionnaires sont plus abondants en général chez le jeune (Tableau 5). La convergence est de 46 temporo-dorsalement chez l'adulte, et de 33 dorsalement chez la jeune limande.

20. *LOPHIUS AMERICANUS* (FIG. 31, 63)

Les cônes de la couche visuelle sont relativement très gros et peu nombreux. Aucune zone rétinienne ne contraste vraiment avec ses voisines en ce qui touche la densité des cônes. Toutefois un faible maximum est observé en zone temporo-dorsale (Fig. 1D). Les cônes sont simples, doubles symétriques et triples dans toutes les régions examinées, et quelques quadruples sont trouvés temporo-ventralement et nasalement. Chaque composante du cône triple a la même taille que la composante d'un cône double, et il en est de même pour les cônes quadruples. La disposition spatiale des cônes se réduit essentiellement à une seule mosaïque commune à toutes les zones étudiées (Fig. 63). Il s'agit de la mosaïque désintégrée du type H.

Les bâtonnets sont relativement peu nombreux en général, et il n'y a pas de grandes variations de densité d'une zone à l'autre. La couche nucléaire interne est très faible en dimensions et en apport d'éléments cellulaires. Les bipolaires, même dans les meilleures zones, sont clairsemées dans une couche un peu floue. Les cellules horizontales et amacrines sont absentes ou difficilement reconnaissables. La couche ganglionnaire n'a pas connu un meilleur sort. Les noyaux ganglionnaires sont très rares dans presque toutes les zones étudiées. La convergence est de 814 dans la zone temporo-dorsale.

DISCUSSION

A partir des observations enregistrées précédemment, il est possible de déduire un modèle morphologique de la rétine pour tous les téléostéens étudiés. La rétine est mixte chez toutes ces espèces, c'est-à-dire qu'elle comporte cônes et bâtonnets dans sa couche visuelle. Elle est donc potentiellement en mesure d'assurer une vie arythmique au poisson, i.e., pas exclusivement diurne ou nocturne. Les cônes doubles sont présents et dominants dans tous les cas. Le pigment épithélial est également présent dans toutes les rétines, et dans toutes les zones rétiniennes.

L'abondance relative des cônes et des bâtonnets peut varier très fortement entre les différentes espèces, mais aussi à l'intérieur d'une même rétine. Au niveau interspécifique, les cônes sont particulièrement bien représentés chez les Clupeidae *Alosa* et *Clupea*, chez *Tautogolabrus*, *Triglops*, et les pleuronectes *Glyptocephalus* et *Limanda*. Ces éléments photopiques sont nécessaires chez des poissons pélagiques côtiers tels les deux premières espèces, ou chez un poisson typique du littoral comme *Tautogolabrus*. Les deux dernières espèces sont des habituées des fonds du plateau continental, souvent à de bonnes profondeurs. Ceci semble contredire le développement de leurs cônes. Mais il doit être tenu compte que les pleuronectes exécutent possiblement des migrations verticales plus ou moins prononcées, et que les espèces benthiques montrent divers degrés d'activité. D'autre part, le modeste développement des cônes chez plusieurs espèces (*Lycodes*, *Lophius*, *Myoxocephalus*, *Cyclopterus*, Agonidae) s'accorde bien avec un habitat peu éclairé comme celui des fonds de 40–60 brasses du plateau continental. La situation des Osmeridae étudiés nous apparaît intermédiaire, en ce que le nombre de cônes est approprié à une vie en conditions lumineuses diverses. Chez *Mallotus* et *Osmerus*, une qualité rétinienne favorisant la vision photopique semble justifier leur formation en bancs.

Les bâtonnets sont généralement abondants chez les espèces étudiées, et plus particulièrement chez *Alosa*, *Clupea*, *Myoxocephalus* et les pleuronectes. Leur présence ne semble pas tant tenir à une question d'habitat qu'à une simple disponibilité fonctionnelle en fonction des moeurs mêmes de l'espèce considérée. Dans certains cas il pourrait s'agir d'une activité crépusculaire. Mais ce qui paraît plausible, c'est que l'abondance relative des bâtonnets est inversement proportionnelle à celle des cônes. Cette situation est évidente, par exemple, chez *Mallotus*, *Osmerus* et *Tautogolabrus*, comparés à *Lycodes*, *Myoxocephalus*, *Agonus* et *Aspidophoroides*. Elle apparaît donc comme le reflet morphologique d'une constatation d'un autre ordre, voulant que les éléments scotopiques (bâtonnets) fonctionnent lorsque les éléments photopiques (cônes) cessent leur activité sous faible condition lumineuse, et vice-versa (Walls, 1942). Les exceptions apparentes que constituent le hareng, le gaspareau et les pleuronectes s'expliquent facilement si on considère la forte spécialisation topographique de leur rétine. Nous verrons alors que la zone où l'on trouve un maximum de cônes est celle qui montre le plus souvent un minimum de bâtonnets, et vice-versa.

Il serait d'ailleurs avantageux de s'attarder sur les variations régionales que présentent les cônes et les bâtonnets dans une même rétine, afin d'en dégager une signification éventuelle. Chez *Alosa* et *Clupea*, les cônes sont beaucoup plus nombreux et plus minces dans une aire très locale de la rétine que dans toute autre zone, et inversement pour le nombre de bâtonnets. Une telle aire ou area retinae fut localisée ventralement chez le gaspareau et temporo-ventralement chez le hareng (Fig. 1). Ce genre de spécialisation, tout comme la fovea plus rare des téléostéens (Kahmann, 1936; Schwassmann, 1968) où n'apparaissent que des cônes simples, est généralement relié à une augmentation brusque de l'acuité visuelle. Depuis le travail de Tamura (1957) dans lequel il met en parallèle la direction de l'accomodation du cristallin et l'area retinae chez plusieurs poissons, il nous est permis de supposer que l'axe visuel est pointé sur l'area retinae en passant par le centre du cristallin. Les travaux subséquents de Tamura et Wisby (1963) et Kimura et Tamura (1966) l'ont confirmé. Cet axe primaire serait donc orienté vers le haut chez le gaspareau, et vers l'avant en pente ascendante chez le hareng. Un tel dispositif est conciliable avec les habitudes trophiques de ces deux Clupeidae. En effet, ils se nourrissent surtout de plancton en s'élançant vers l'avant et au-dessus de leur corps où abondent les proies. De cette façon, l'axe visuel primaire peut servir à fixer la proie efficacement au moment crucial de la poursuite. Tamura et Wisby (1963) ont trouvé que l'axe visuel de quelques poissons pélagiques (thons) a une orientation telle que décrite ici. Par contre, l'orientation de l'axe était nettement horizontale, vers l'avant, chez le sériole, le dauphin et le grand barracuda.

Parmi les autres espèces étudiées, plusieurs retiennent l'attention par la présence d'une area retinae, mais cette aire n'est jamais aussi bien définie que celle des Clupeidae. Nous devons tenir compte du fait que la localisation de cette zone spécialisée est basée sur un nombre moins élevé de régions rétiniennes examinées. De plus, certaines de ces rétines ne comportent qu'un nombre plutôt faible de cônes, ce qui nous oblige à soulever des réserves quant à l'efficacité d'une area quelconque chez ces espèces.

La localisation ventrale ou temporo-ventrale de l'area retinae chez les Osmeridae (capelan et éperlan) s'accorde au fait que ces poissons, comme les Clupeidae précédents, se nourrissent principalement de plancton. L'area est également ventrale et un peu temporo-ventrale chez *Cyclopterus*, dont les moeurs sont plutôt sédentaires sur les fonds rocheux. Ces faits ne sont pas incompatibles, car leurs proies sont le plus souvent pélagiques, et forcément situées au-dessus d'un prédateur parfois semi-pélagique. *Triglops*, dont l'area est nettement temporo-ventrale, présente une situation passablement analogue. Si l'on tient compte de la position de l'oeil droit chez la plie *Glyptocephalus* et celle de son area retinae, nous pouvons détecter un axe visuel primaire à orientation légèrement latérale et en biais vers le haut où se trouvent les petits invertébrés dont se nourrit ce poisson benthique. D'autre part, la localisation de l'axe visuel selon l'horizontale et vers l'avant chez la limande adulte permet sans doute à ce pleuronecte benthique et sédentaire de se nourrir des petits crustacés et poissons situés au niveau des fonds de 30–60 brasses. Le déplacement de l'axe d'environ 45° vers le pôle dorsal rétinien chez la jeune limande est probablement imputable au fait que ses yeux n'occupent pas encore leur position définitive.

La localisation temporo-dorsale de l'area chez trois lycodes (*L. lavalei*, *L. reticulatus*, *L. turneri*) leur permet d'inspecter les fonds du plateau continental en quête de divers invertébrés et petits poissons, grâce à un champ visuel primaire dirigé en biais vers le bas. Toutefois, le faible nombre de cônes qui leur est propre limite leurs possibilités visuelles. L'axe n'est utile, et encore modestement, que si l'animal se meut lentement. Deux autres lycodes (*L. vahlii*, *Lycodes* sp.) ont une area plus temporale, mais cela ne saurait modifier profondément le comportement décrit ci-dessus. L'axe visuel est enligné horizontalement avec la zone rétinienne temporale chez plusieurs autres poissons plus ou moins benthiques du plateau (*Myoxocephalus*, *Aspidophoroides*, et peut-être *Agonus*). Ces poissons errent droit devant à la recherche d'invertébrés ou d'autres matières organiques du benthos, et il est donc plausible que l'axe leur soit de quelqu'utilité. Ainsi en est-il de l'axe horizontal d'*Eumesogrammus* qui semble se nourrir plutôt d'organismes semi-pélagiques.

Chez deux espèces, une area retinae est complètement inexistante, et ce pour des raisons différentes, semble-t-il. Chez *Tautogolabrus*, la plupart des régions rétiniennes abondent en cônes, avec un faible maximum entre le fundus et la périphérie temporale. De plus, non seulement les cônes simples sont-ils aussi nombreux que les doubles, mais ils se sont différenciés en deux types. Un tel dispositif semble exclure la présence d'un axe visuel *primaire*, ce qui nous laisse à penser que la rétine entière est *fonctionnellement* comparable à l'area des Clupeidae, étant donné son bon développement. O'Connell (1963) a trouvé une carence semblable d'area définie chez deux maquereaux et il a suggéré que leurs yeux font probablement des mouvements rapides et extensifs afin de stabiliser un milieu visuel (écran des images) fort changeant. Ce comportement oculaire fut observé en aquarium par le présent auteur chez *Tautogolabrus*. Ce poisson du littoral vit à proximité des fonds où il dévore un grand nombre de Crustacés.

Chez la baudroie *Lophius*, si l'on se réfère à la rareté relative et à la grande taille des cônes, la rétine apparaît très pauvrement développée dans toute son étendue. En pareille circonstance, il serait difficile d'imaginer un dispositif qui remplacerait l'axe visuel primaire, car l'acuité visuelle n'est pas impliquée ici. La baudroie est une habituée sédentaire des fonds du plateau continental, pouvant aller de la zone des marées jusqu'à plus de 300 brasses. Il semble acquis que l'axe visuel doit présenter peu d'intérêt à un poisson si peu actif, parce que le besoin de fixer mécaniquement une proie n'est guère évident.

Comme l'a déjà fait remarquer Rochon-Duvigneaud (1943), on ne doit pas se faire trop d'illusions au sujet de l'acuité visuelle chez les poissons, surtout à cause du milieu aquatique qui est leur décor. Les propriétés dispersantes de l'eau réduisent la capacité de résoudre les images (Nicol, 1963). A partir des résultats, l'acuité visuelle rétinienne fut néanmoins estimée d'après la méthode de Tamura (1957). Cette mesure nous est donnée par l'angle de résolution minimum, excluant l'hypothèse que les points d'image peuvent être résolus seulement lorsqu'ils tombent sur des cônes séparés par au moins un cône non stimulé. La formule utilisée est la suivante:

$$\frac{1}{F}\left[\frac{0.2\ (1 + 0.25)}{\sqrt{n}}\right] = \text{angle minimum en radians}$$

où F, distance focale du cristallin; n, nombre maximum de cônes par 0.04 mm^2; 0.25, degré de rétraction du tissu traité. F est calculé d'après le rayon du cristallin selon la règle de Matthiessen ($F = 2.55 \times$ rayon). De plus, le niveau de spécialisation topographique des rétines principalement étudiées fut calculé parallèlement. Il s'agit du quotient obtenu en divisant le nombre maximum de cônes de l'area retinae par la moyenne des comptes de toutes les autres zones rétiniennes. L'ensemble de ces données est fourni dans le Tableau 7.

D'après les données, il existe une faible relation inverse entre le degré d'acuité visuelle (pouvoir de résolution) et le degré de hiérarchie topographique dans la rétine, i.e., présence d'une area plus ou moins définie. Ceci suggère qu'en termes de qualité visuelle l'existence d'une area retinae ne présente qu'un avantage relatif. Relatif, car la qualité visuelle d'une rétine à faible niveau de spécialisation peut dépendre de l'abondance des cônes (*Tautogolabrus, Cyclopterus*) ou du développement du cristallin (*Lophius, Lycodes reticulatus, L. vahlii*).

De facon générale, il semble que le pouvoir de résolution concerne plus la rétine que le cristallin chez les poissons (Tamura, 1957). Le même auteur semblait indiquer que le rôle de la rétine dans l'acuité visuelle est plus grand chez les rétines de plus grande dimension. D'après nos mesures enregistrées chez *Lycodes reticulatus* et *Limanda ferruginea*, jeunes et adultes, l'on pourrait supposer que le pouvoir de résolution de la rétine augmente aux dépens du cristallin avec l'âge. Ce phénomène s'explique apparemment par la différenciation progressive de l'area retinae au cours de la croissance. Mais d'autres facteurs doivent intervenir puisque, selon O'Connell (MS, 1967), l'angle de résolution minimum s'améliore avec l'âge, mais à taux décroissant.

TABLEAU 7. Niveau de spécialisation topographique de l'area retinae et angle de résolution minimum chez les espèces étudiées. La longueur des spécimens est indiquée.

Espèces (*mm*)	Nombre de zones rétiniennes concernées	Niveau de spécilisation	Angle de résolution minimum (*min.*)
A. decagonus (203)	2	1.09	13.0
L. americanus (690)	13	1.44	6.4
L. reticulatus (290)	7	1.49	12.7
C. lumpus (290)	7	1.57	6.7
M. octodecemspinosus (245)	7	1.60	13.2
A. monopterygius (187)	6	1.63	13.5
L. turneri (245)	7	1.64	13.2
T. adspersus (255)	13	1.68	4.7
M. villosus (165)	5	1.75	9.0
L. ferruginea (143)	7	1.81	8.1
L. reticulatus (725)	7	1.86	4.0
M. scorpius (240)	7	2.01	6.1
T. murrayi (127)	7	2.18	6.9
L. lavalei (640)	7	2.22	9.2
L. vahlii (226)	7	2.30	11.8
Lycodes sp. (600)	7	2.30	7.2
E. praecisus (138)	7	2.40	12.0
L. ferruginea (290)	7	2.62	5.0
O. mordax (175)	2	3.00	7.2
G. cynoglossus (435)	7	3.14	3.5
C. harengus (350)	13	4.47	3.7
A. pseudoharengus (340)	13	5.15	4.5

Certaines des mesures ne sont pas adéquates. Cela est évident en ce qui touche *Agonus* et *Osmerus*, à cause du nombre trop faible de zones examinées. Toutefois, certaines tendances peuvent être décelées, en se rappelant que nous comparons des spécimens adultes. Les habitués des fonds peu éclairés du plateau continental montrent le plus souvent une rétine à faible niveau de spécialisation et à pouvoir de résolution modéré. Par contre, les espèces typiquement côtières, pélagiques ou du littoral, faisant face à un milieu plus éclairé, sont pourvues d'une rétine à acuité visuelle plus élevée, quel que soit le niveau de spécialisation (*Tautogolabrus* vs *Clupea* et *Alosa*). Une curieuse exception est celle des pleuronectes adultes qui possèdent une structure rétinienne remarquable, malgré leur habitat relativement sombre et leur faible activité. Ici il est probable que des variations journalières de l'activité trophique interviennent, comme peuvent le suggérer les données de Beamish (1966), variations qui régulariseraient l'usage modéré d'une bonne vision dans un tel milieu. Une seconde possibilité à considérer est la très faible proportion des cônes simples dans l'area retinae, ce qui ne peut que limiter la qualité visuelle dans une certaine mesure (Tableau 5).

Du point de vue de la comparaison, les conclusions auxquelles nous sommes arrivés sur l'acuité visuelle sont probablement valides. Mais il doit être entendu qu'en termes absolus les valeurs du Tableau 7 ne sont pas précises. La véritable valeur de l'acuité visuelle, ou celle qui s'en approche le plus, est plus pertinemment mesurée en étudiant le comportement. L'angle de résolution déduit de ces études est généralement plus grand que celui obtenu à partir de l'abondance des cônes (Yamanouchi, 1956; Nakamura, 1968).

NEURONES ET NÉVROGLIES DE LA RÉTINE

Si nous considérons maintenant les couches internes de la rétine, et plus particulièrement les différentes couches nucléaires, il nous apparaît possible de relier le développement de la couche visuelle à celui des éléments nerveux sous-jacents. D'une façon générale, l'abondance relative des neurones (cellules bipolaires et ganglionnaires) suit parallèlement celle des cônes. Ceci est vrai tant au niveau intrarétinien, où l'area retinae est souvent très riche en éléments nerveux, qu'au niveau interspécifique. La démonstration en est donnée, par exemple, si l'on compare les différentes zones rétiniennes du gaspareau, ou si l'on compare les couches internes des lycodes et de la baudroie à celles du hareng et de la tanche-tautogue. Cette corrélation a maintes fois été formulée dans le passé à partir d'espèces pélagiques (O'Connell, 1963) ou benthiques (Ali et Hanyu, 1963; Ali et al., 1968). Elle implique qu'une plus grande abondance de neurones par rapport à l'abondance des cônes facilite une intégration rétinienne plus raffinée et, peut-être, une meilleure acuité (O'Connell, 1963).

Au niveau de la couche nucléaire interne, les cellules horizontales et amacrines sont généralement beaucoup moins nombreuses que les bipolaires chez toutes les espèces. Particulièrement chez les rétines où les cônes sont faiblement représentés et où les couches internes sont peu développées, ces éléments semblent les premiers à disparaître. Ceci indique probablement qu'ils jouent un rôle accessoire ou complémentaire dans l'élaboration de l'acuité rétinienne. En fait, nos connaissances sur ces cellules sont plutôt fragmentaires. D'après Villegas (1961), les cellules horizontales des poissons pourraient être des névroglies satellites des bipolaires. Et selon Villegas et Villegas (1963), les cellules amacrines peuvent être du type neurone ou du type névroglie, tandis que Selvin de Testa (1966) en reconnaît plusieurs sortes qui seraient morphologiquement intermédiaires entre le neurone et la névroglie typiques. Cette dernière vue semble la plus acceptable en fonction de nos observations. Le rôle accessoire imaginé ci-dessus pourrait évidemment consister à informer les systèmes photopique et scotopique sur une base collatérale plutôt que transversale (cellules visuelles → bipolaires → ganglionnaires). Les cellules horizontales le feraient pour les cellules visuelles, et les amacrines pour les bipolaires et les ganglionnaires. D'ailleurs, Stell (1967) a déjà reconnu deux sous-systèmes de cellules horizontales chez *Carassius auratius*: un faisant synapse avec les cônes, et l'autre avec les bâtonnets. Un pareil dispositif est possible chez *Tautogolabrus*, où une dentelure nucléaire fut observée au-dessus de la couche classique des cellules horizontales.

Les rapports numériques entre les cellules visuelles et ganglionnaires (convergence ou sommation) font preuve d'une très grande variabilité chez les espèces étudiées. Parallèlement à l'abondance des cellules visuelles et nerveuses, cette variabilité se fait sentir fortement à l'intérieur même de la rétine et, comme prévu, l'area retinae possède généralement la convergence la plus faible. Il est donc probant que du degré de sommation dépend l'importance accordée au pouvoir de résolution rétinien chez l'espèce étudiée. Au niveau interspécifique, il existe une corrélation très nette entre l'acuité visuelle telle qu'estimée précédemment et le degré de sommation minimum; ou encore entre l'habitat et les moeurs de l'espèce et le degré de sommation. Les valeurs de la convergence chez les espèces pélagiques côtières (hareng, gaspareau) s'apparentent d'ailleurs à celles des poissons pélagiques étudiés par O'Connell (1963), valeurs déduites par Munk (1965).

LES CÔNES: TYPES ET MOSAÏQUES

Comme l'a déjà indiqué Engström (1963c), l'étude combinée des variations morphologiques et topographiques des cônes fournit une information valable sur les adaptations fonctionnelles régionales de la rétine. D'après nos résultats, il semble que l'inventaire des formes de cônes et de leurs arrangements réflète assez bien la qualité visuelle d'une rétine telle qu'estimée précédemment.

Les cônes simples sont trouvés chez presque toutes les espèces, et leur taille peut varier beaucoup. Chez les espèces pélagiques côtières qui possèdent une area retinae très saillante (*Alosa*, *Clupea*, *Osmerus*), les cônes simples sont curieusement rares ou absents dans les autres zones rétiniennes. Chez les poissons dont toute la rétine semble faire office d'area (*Tautogolabrus*), les cônes simples sont plus abondants, et ce dans toute la rétine. Chez les rétines à faible acuité (*Lycodes*, *Lophius*), les cônes simples sont rares dans toutes les zones. Ces faits suggèrent sans équivoque que ce type de cône est associé à des conditions lumineuses excellentes (vision photopique) chez ces poissons. Plus spécifiquement, ces cônes sont associés à une bonne acuité visuelle, car ils sont encore abondants dans l'area retinae des pleuronectes. Leur absence totale chez *Mallotus* ou virtuelle chez *Agonus* n'étonne pas, si l'on tient compte de l'habitat de ces deux espèces, lequel est même généralement beaucoup plus profond que notre site de capture chez *Agonus*.

Les cônes doubles sont communément rencontrés chez toutes les espèces, et ils dominent chez toutes ces espèces. Toutefois, ils égalent souvent en nombre les cônes simples chez *Tautogolabrus*, un poisson du littoral habitant les zones superficielles. Il n'existe pas de véritable évidence, dans le présent travail, quant à l'association des cônes doubles à un habitat généralement plus sombre. Ce fut aussi le cas dans le travail de Tamura et Wisby (1963). Une telle association n'est cependant pas à exclure, car certains travaux ont tendu à la révéler (Tamura, 1957; Ali et Hanyu, 1963). Mais la démonstration en a souvent été affaiblie par l'utilisation unique de coupes transversales. D'un autre côté, la présence des cônes doubles asymétriques est plutôt sporadique chez une espèce, et leur distribution parmi les groupes phylogéniques ne semble pas se faire selon des règles définies. Cette conclusion est latente dans Engström (1963b), qui a montré à ce point de vue les nombreuses contradictions des auteurs précédents. En termes fonctionnels, il est possible que les deux composantes du cône double asymétrique soient dotées d'une sensibilité différente à la lumière, comme le laisse croire le comportement photomécanique des deux composantes en état d'apdatation à l'obscurité chez *Agonus*. Mais il est difficile de voir quel avantage le poisson retirerait d'un tel mécanisme. Ajoutons que Willmer (1953) semble croire que le cône double comporte au moins une composante à sensibilité intermédiaire, se rapprochant de celle du bâtonnet. Il est également possible que fonctionnellement les cônes doubles plus larges des zones rétiniennes non spécialisées répondent différemment à un même stimulus lumineux, car le volume occupé par le pigment visuel change forcément. Ceci est plausible puisque les zones non spécialisées devraient se distinguer de l'area retinae par une augmentation correspondante de la sensibilité visuelle.

Les cônes triples n'ont été enregistrés que chez environ quarante espèces jusqu'ici (Engström, 1963b). Le présent travail comporte plusieurs espèces chez lesquelles ces cônes sont signalés pour la première fois. Chez certaines espèces (*A. pseudoharengus*, *M. scorpius*, *L. ferruginea*), les cônes triples sont concentrés dans une aire minuscule de la rétine. Chez d'autres (*Lycodes*, *Agonus*, *Lophius*), ils sont plus dispersés, et parfois même présents partout dans la rétine. Sachant que ces derniers possèdent une rétine morphologiquement pauvre on peut avancer l'idée que le mode de distribution des cônes triples dans la rétine aura une grande portée sur la valeur de l'acuité visuelle. Pour faire suite, signalons que même des cônes quadruples ont été observés à l'occasion, constitués en forme de carrés. Ils sont trouvés très localement chez *M. scorpius*, mais sont présents dans plusieurs zones rétiniennes chez *Lycodes turneri* et *Lophius americanus*. Auparavant, ils ont été localisés chez seulement cinq espèces de téléostéens (Lyall, 1957; Engström, 1963b). Il nous manque encore beaucoup d'information sur ces cônes, mais on peut supposer à ce stade que leur mode de distribution dans la rétine est analogue à celui des cônes triples, et conséquemment leur fonction aussi. Cette hypothèse est renforcée par le fait que ce type de cônes côtoie invariablement les cônes triples chez toutes les espèces qui le possèdent.

La disposition spatiale des différents types de cônes peut être envisagée de deux façons. D'abord, au niveau phylogénique, aucun grand groupe ne semble avoir retenu un type de mosaïque spécialisé qui lui soit propre. La mosaïque A du Labridae *Tautogolabrus* constitue l'exception, et on peut la considérer comme très avancée. D'ailleurs elle a probablement été retenue par toute la famille des Labridae, comme l'indiquent les observations de Engström (1963a). Toutefois, si l'on tient compte des variations intrarétiniennes de la mosaïque, il est alors possible de reconnaître certaines tendances propres à un grand groupe. Chez les Clupéiformes (*Alosa*, *Clupea*, *Mallotus*, *Osmerus*), groupe primitif, la mosaïque B carrelée à cône simple central n'est retenue que par une ou deux zones rétiniennes, toujours les plus spécialisées. La mosaïque qui domine ce groupe dans la majeure partie de la superficie rétinienne est du type E ou F selon leur qualité visuelle. Par contre, chez les Perciformes (Stichaeidae, Cottidae, Agonidae, Cyclopteridae), la mosaïque carrelée B est répandue parmi un plus grand nombre de zones rétiniennes, et les rangées parallèles E et F sont peu fréquentes. Or, ce dernier groupe est évolutivement beaucoup plus avancé que le précédent.

D'un autre côté, le niveau écologique s'est révélé beaucoup plus déterminant pour expliquer la variabilité des mosaïques à partir d'un type phylogénique. Chez les Perciformes, les zones rétiniennes les moins spécialisées tendent surtout à faire un compromis entre les carrés des areae retinae et les rangées parallèles, et nous obtenons ainsi les mosaïques C et D qui forment des quadrilatères à 45°. Le rôle suppléant joué par la mosaïque C dans l'acuité est démontré par sa présence dans l'area retinae de *Triglops*, où le type carrelé B est absent de toute la rétine. Il s'agit donc d'une étape vers la formule moins sophistiquée des rangées parallèles, puis des mosaïques désintégrées. Un autre groupe évolué, les pleuronectes, a développé le même genre de dispositif, comme tend aussi à le montrer le travail de Engström et Ahlbert (1963). Chez certains Perciformes à faible acuité visuelle (*Lycodes*) et chez *Lophius*, la mosaïque F avec cônes simples occasionnels est parfois conservée dans l'aire rétinienne à maximum de cônes, mais le reste de la rétine doit se contenter d'une mosaïque désintégrée. Cette dernière semble d'ailleurs l'apanage de toute structure rétinienne faible, y compris les zones faibles très locales de certaines espèces à qualité visuelle satisfaisante (*Alosa*, *Myoxocephalus*, *Limanda*). Il est remarquable que l'aire désintégrée de *M. scorpius*, et surtout de la jeune *Limanda*, se situe au voisinage de l'area retinae. La même situation s'est présentée chez quelques pleuronectes étudiés par Engström et Ahlbert (1963). Il est même possible que nous l'ayons escamotée chez la limande adulte et chez la plie grise. Un tel arrangement a peut-être l'avantage de fixer plus sûrement l'axe visuel primaire, en produisant un fort contraste avec la zone rétinienne voisine.

La distribution des mosaïques parmi les espèces étudiées supporte l'idée de Lyall (1957) et Engström (1963b) voulant que les mosaïques les plus élaborées soient des dispositifs spécialisés pour la perception des objets à mouvement rapide. L'exemple le plus probant est fourni par *Tautogolabrus*, dont les habitudes de vie se fondent largement sur la vision. Lyall (1957) suppose que ces dispositifs assignent inévitablement une distribution uniforme aux différents types de cônes. Cette distribution serait plus justifiée si, aux types morphologiques de cônes, correspondent des types physiologiques. Les travaux de Marks (cité par MacNichol, 1964) et Lang (1967) suggèrent une telle corrélation, en associant différents types de cônes à des régions différentes du spectre visible. Cependant, des travaux encore plus raffinés de cette sorte s'avèrent nécessaires avant de formuler des corrélations définitives. Ces mêmes travaux nous permettraient sans doute de vérifier l'opinion apparemment fondée selon laquelle les cônes doubles, triples, et quadruples seraient intermédiaires (dans l'ordre) en sensibilité spectrale entre les cônes simples (photopiques) et les bâtonnets (scotopiques).

CONCLUSIONS

(1) L'étude détaillée de la structure rétinienne, entreprise chez quelques téléostéens pélagiques et benthiques du plateau continental, nous a permis de relier l'environnement lumineux et le mode de vie de ces poissons à la qualité de leur appareil visuel.

(2) D'une facon générale, l'abondance relative des bâtonnets est inversement proportionnelle à celle des cônes dans la couche visuelle. Cette relation se vérifie tant au niveau interspécifique qu'au niveau des zones d'une rétine.

(3) La spécialisation topographique des cônes dans la rétine, ou formation d'une area retinae, est plus marquée chez des espèces pélagiques actives (*Clupea*, *Alosa*); elle est moins prononcée chez les espèces benthiques moins actives. Elle est inexistante chez *Tautogolabrus*, mais un dispositif compensateur semble intervenir chez cette espèce.

(4) Le pouvoir de résolution des images dans l'area retinae augmente avec l'âge chez deux espèces (*Lycodes*, *Limanda*). Il est plus élevé chez les espèces pélagiques (Clupeidae) ou du littoral (*Tautogolabrus*), et diminue chez les espèces benthiques.

(5) D'une facon générale, l'abondance relative des neurones des couches rétiniennes internes suit parallèlement celle des cônes, tant interspécifiquement que dans une même rétine. L'importance accordée au pouvoir de résolution dépend largement du degré de sommation des photorécepteurs au niveau des bipolaires et ganglionnaires.

(6) Le distribution des différents types de cônes à l'intérieur d'une même rétine suggère que leur sensibilité à la lumière est plus grande à mesure que l'on passe du cône simple au cône quadruple, puis au bâtonnet.

(7) Certaines tentances phylogéniques sont décelées en ce qui a trait aux modes de distribution des mosaïques à cônes. De plus, la disposition spatiale des types de cônes est plus raffinée chez les espèces actives qui sont susceptibles de détecter les objets à mouvement rapide.

REMERCIEMENTS

L'auteur exprime sa vive reconnaissance au Professeur M. A. Ali pour les suggestions et les critiques qu'il a formulées en supervisant le présent travail. L'aide technique du Gouvernement du Québec, et plus spécifiquement celle du Dr Alexandre Marcotte à la Station de Biologie Marine, Grande-Rivière, Qué., fut pleinement appréciée lors du séjour de l'auteur à la dite station. La collaboration de M Jean Garneau et Mmes A. Darkazanli et H. Farid a rendu possible la réalisation des photographies et des dessins.

L'aide financière du Conseil National de Recherches du Canada s'est manifestée sous forme d'une bourse post-grade à l'auteur, et d'une subvention au Dr M. A. Ali.

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Isolation and Preliminary Characterization of Some *Aeromonas salmonicida* Bacteriophages[1]

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PATERSON, W. D., R. J. DOUGLAS, I. GRINYER, AND L. A. McDERMOTT. 1969. *Isolation and preliminary characterization of some Aeromonas salmonicida bacteriophages.* J. Fish. Res. Canada 26: 629–632.

Bacteriophages for *Aeromonas salmonicida* were isolated from water and mud samples taken from 13 of 19 trout hatcheries and ponds examined in southern Ontario. Nine of the 13 locations were known to have histories of furunculosis disease. The bacteriophages studied formed three serological groups and two distinct morphological types. Phages of serological groups I and II possessed similar morphology; those of group III resembled the coli T-even phages. All possessed complex symmetry consisting of a head and tail with a contractile tail sheath. Latent periods of the phages ranged from 35 to 95 min and average burst sizes from 21 to 193. A group I phage and a group III phage had $S^0_{20,w}$ values of 351 and 1000, respectively.

Received November 13, 1968

INTRODUCTION

FURUNCULOSIS is an important disease of fish in many countries of the world. Excellent reviews of the disease and its causative agent, *Aeromonas salmonicida*, are available (McCraw, 1952; Herman, 1968).

Isolations of bacteriophages for *A. salmonicida* were reported in Great Britain during the 1930's (Furunculosis Committee, 1933, 1935; Todd, 1933; Christison et al., 1938), but little information on them was obtained at the time nor has any appeared in the literature since. This report describes some of the properties of *A. salmonicida* phages isolated from trout hatcheries and ponds in southern Ontario.

MATERIALS AND METHODS

Water or mud samples, or both, from 19 trout pond and hatchery effluents were examined for *A. salmonicida* bacteriophages. Brain heart infusion (Difco) was employed for the routine cultivation, dilution, and enumeration of the bacteria and phage strains.

A culture of *A. salmonicida* in the logarithmic phase was added to the sample and the mixture incubated at 26 C for 2–3 days. Samples (10–15 ml) of the supernatant solution were removed, clarified by centrifugation at 5000 *g* for 40 min, then filtered through Millipore filters of 0.45-mμ pore size.

Detection and enumeration of phages were achieved using brain heart infusion agar and the double agar layer technique of Adams (1959). The plates were examined for phage plaques

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Printed in Canada

after an incubation period of 24 ± 4 hr at 26 C. Isolated plaques were picked with a sterile loop or sterile Pasteur pipette and replated after dilution in brain heart infusion broth. Phage preparations were considered pure after four to five such serial single plaque isolations.

Phage suspensions of high titre were prepared according to the methods of Adams (1959) using both broth lysates and confluently lysed plates. The phages were concentrated and partially purified by a modification of the differential centrifugation procedure outlined by Adams (1959) and Bradley (1967). Coarse materials from broth lysates or from harvested confluent plates were sedimented at 5000 *g* for 40 min. Cells in the supernatant were then removed by centrifugation at 10,000 *g* for 20 min. Phage particles in the final supernatant were pelleted by centrifugation at 105,000 *g* for 120 min or 144,000 *g* for 40 min. The phage pellets were allowed to become suspended overnight in 0.1 M sodium chloride or 0.1 M ammonium acetate, both at *p*H 7.0.

Antisera against eight phages were prepared in rabbits according to the procedure of Leskowitz and Waksman (1960). The inoculum consisted of equal volumes of Freund's adjuvant and *A. salmonicida* phage suspension (10^{10}–10^{12} plaque-forming units/ml) in physiological saline. Two subcutaneous injections were administered into the rear foot pads and into the nape of the neck at 3–5-week intervals. Serum inactivation rates of homologous and heterologous phages were calculated as described by Adams (1959). For comparison values, K′ values (the ratio of the heterologous K value to the homologous K value) were determined (Scott, 1965); for the homologous system, $K' = 1.0$.

One-step growth experiments were conducted and the latent period and burst size for representative phages of each serological group were determined at 26 C using the procedure outlined by Adams (1959).

Representative phages from each serological group were negatively stained by the method described by Brenner and Horne (1959). The grids were examined with the Phillips EM 200 electron microscope using double condenser illumination.

The sedimentation coefficient ($S^0_{20,w}$) of a representative of each of the two morphological phage types was determined in a Beckman Model E ultracentrifuge with schlieren optics at a rotor speed of 15,000 rpm.

RESULTS AND DISCUSSION

Bacteriophages for *A. salmonicida* were isolated from 37 of the 58 water and mud samples examined. The positive samples came from 13 of the 19 trout hatcheries and ponds surveyed, and 9 of these locations had histories of furunculosis disease. The phages were isolated during all seasons of the year and with equal frequency from water and mud.

Figure 1 shows the plaque morphology of some of the phages. The plaques ranged from 0.1 to 2.0 mm in diameter. They were relatively clear but a variation in lytic ability was evident.

The results of the neutralization of the *A. salmonicida* phages by antisera are presented in Table 1. There were three serological groups, and although some overlapping did occur between phages of groups I and II, phages in group III were serologically distinct.

One-step growth curves of four of the phages are shown in Fig. 2. The latent period and average burst size of each of the same phages are given in Table 2.

Electron micrographs of negatively stained preparations of some of the *A. salmonicida* phages are shown in Fig. 3 and 4. Phages 37, 56RR2, and 59.1, members of serological group I or II, are similar in appearance each possessing a head with cubical symmetry and a rigid tail with a contractile tail

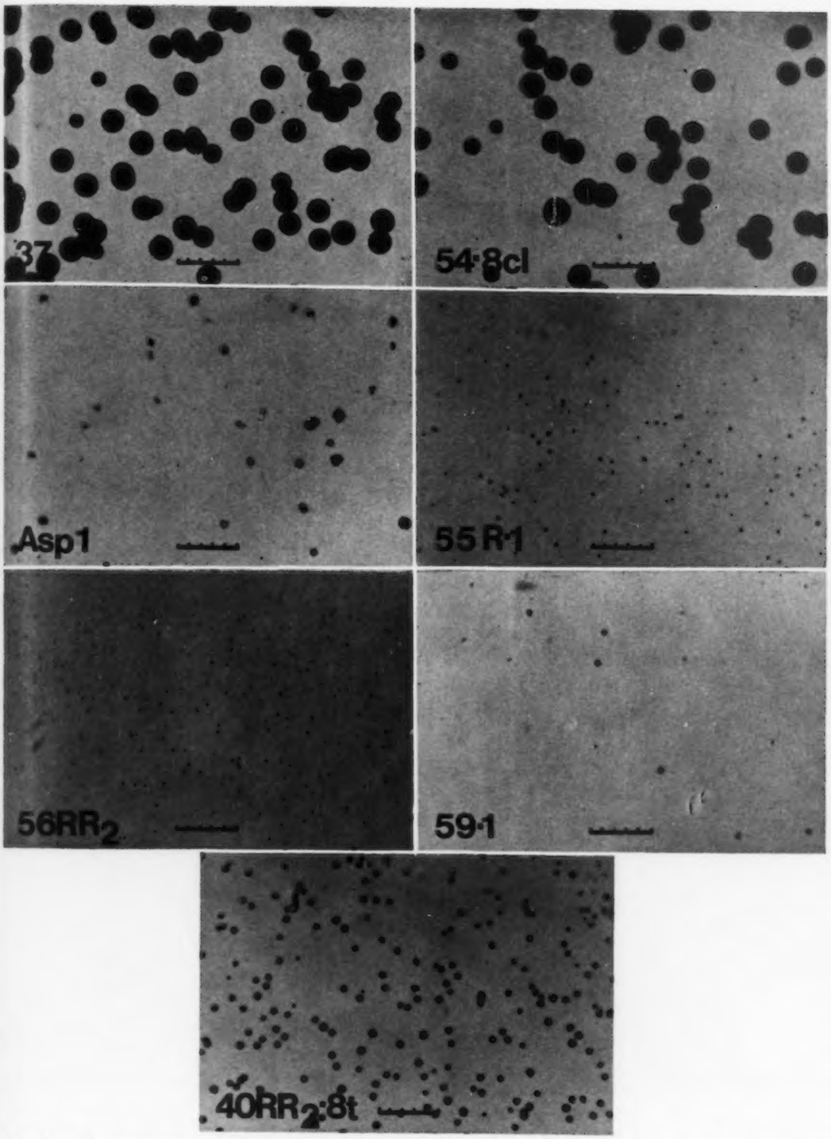
37
54·8cl
Asp1
55R1
56RR2
59·1
40RR2:8t

FIG. 1. Plaque morphology of some *Aeromonas salmonicida* bacteriophages. Scale = 5 mm.

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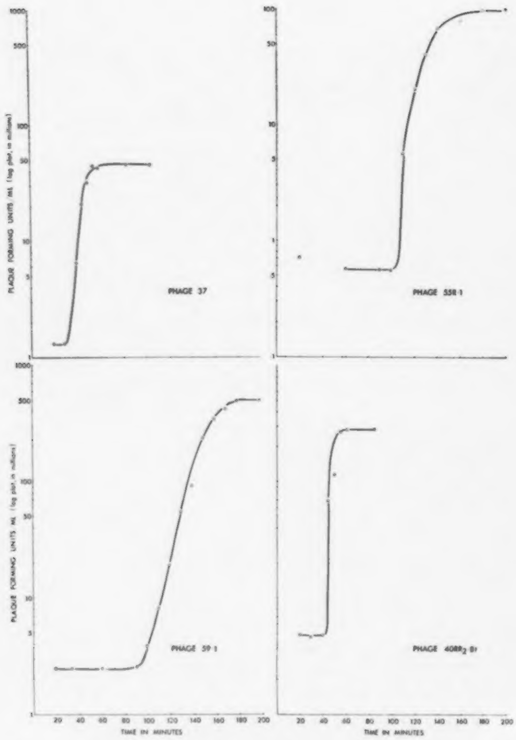

FIG. 2. One-step growth curves of some *Aeromonas salmonicida* bacteriophages.

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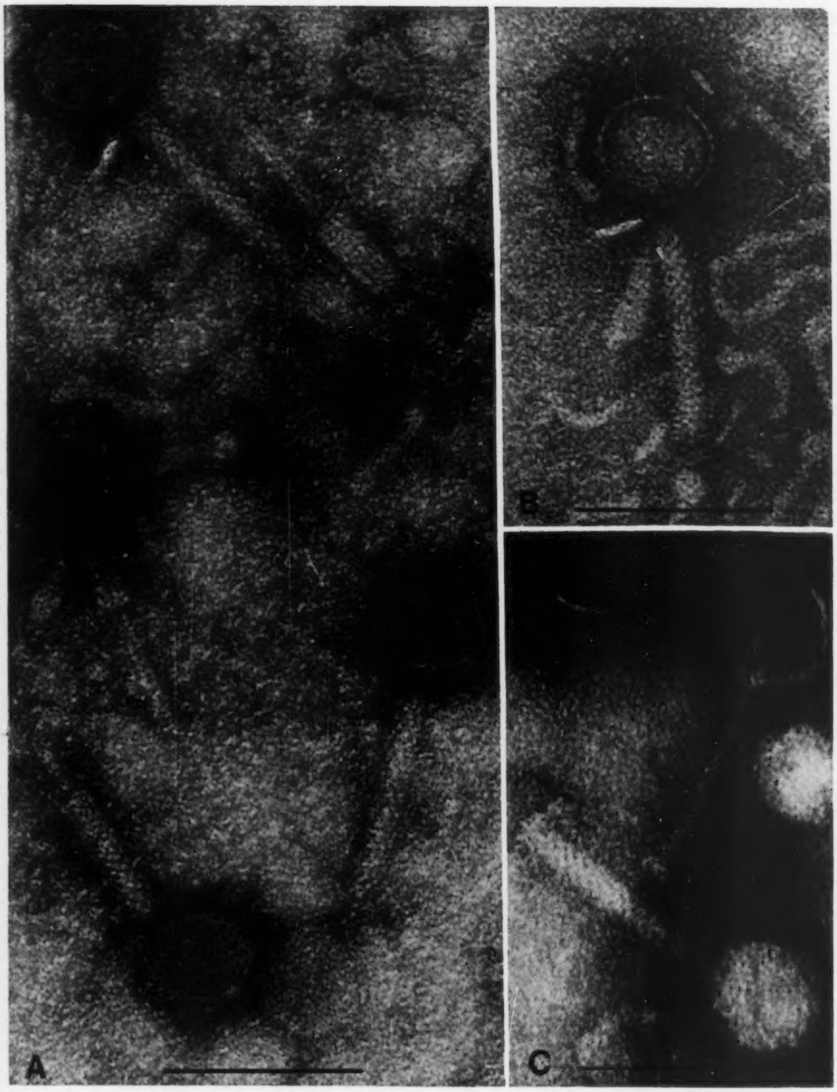

FIG. 3. Electronmicrographs of *Aeromonas salmonicida* bacteriophages, serological groups I and II. A, phage 37 (group I); B, phage 56RR2 (group II); C, phage 59.1 (group II). Scale = 1000 Å.

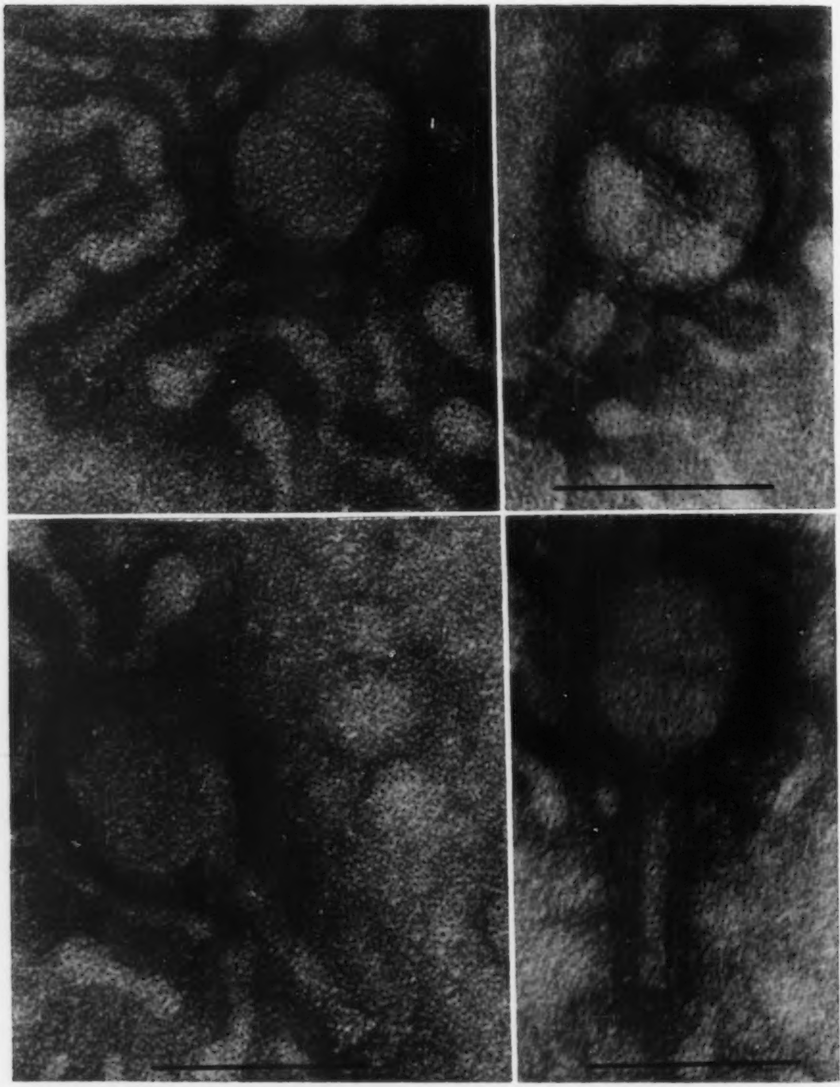

FIG. 4 Electronmicrographs of *Aeromonas salmonicida* bacteriophage 40RR2.8t, serological group III. *p* = base plate and tail fibres; * = contracted tail sheath; *c* = collar; *f* = fibrous network. Scale = 1000 Å.

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TABLE 1. Rates of neutralization of *Aeromonas salmonicida* phages by antisera.

Phage	Serological group	Homologous K	K′ values with antiserum to phage: Asp 1	37	54.8cl	56RR2	59.1	40RR2.8t
Asp 1	I	116	1.00	0.36	0.01	0.00	0.00	0.00
37	I	380	0.97	1.00	0.10	0.19	0.00	0.00
54.8cl	I	63	0.00	0.13	1.00	0.00	0.09	0.00
55R1	II	172	0.00	0.08	0.00	0.23	0.52	0.00
56RR2	II	560	0.00	0.00	0.00	1.00	0.46	0.00
59.1	II	440	0.00	0.03	0.03	0.18	1.00	0.00
40RR2.8t	III	160	0.00	0.00	0.00	0.00	0.00	1.00
44R.8	III	75	0.00	0.00	0.00	0.00	0.00	1.00

TABLE 2. One-step growth characteristics of *Aeromonas salmonicida* phages.

Phage	Latent period (*min*)	Avg burst size
37	35	21
55R.1	95	156
59.1	90	193
40RR2.8t	40	128

sheath. The head, measuring 600–700 Å in diameter, appears to be icosahedral or octahedral in shape. The tail sheaths show capsomere structures distributed in random fashion. The tail measures 1140–1300 Å in length and possesses a base plate. Figure 3C shows a phage particle with the tail sheath removed to reveal the base plate.

Phage 40RR2.8t, representative of serological group III, is similar in morphology to phage T2 of the *Escherichia coli* T series. However, in cross-infection tests with phage 40RR2.8t and T-even phages, only homologous infections could be shown. The elongated head of phage 40RR2.8t measures 900 × 1100 Å. It is similar in shape to that of coli T2 phage for which both a bipyramidal prism shape and a bipyramidal hexagonal antiprism shape have been suggested (Bradley, 1965; Moody, 1965). The micrographs of phage 40RR2.8t show the presence of a collar, a tail sheath extended and contracted, and a base plate with tail fibres (Bradley, 1967). The tail measures about 950 Å in length.

The difference in size of the members of the two morphological phage types is exemplified by their sedimentation coefficients. Phages Asp 1 and 40RR2.8t had $S^0_{20,w}$ values of 351 and 1000, respectively.

ACKNOWLEDGMENTS

This work was supported by a grant from the Fisheries Research Board of Canada.

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Age Determination in the White Sucker

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The purpose of this study was to test the reliability of the scale method for determining the age of white suckers. To do so, an alternative method of "aging" was explored, using sections cut from the first four rays of the pectoral fin. Two hundred and fifty white suckers were tagged, and a piece of one pectoral fin was removed before they were released. A year later, 25 were recaptured, and the rays of the remaining pectoral fin were aged. Of the recaptures, 22 showed clearly the addition of one annulus.

Having confirmed the fin-ray method, the age of another 157 suckers was determined by scales and fin rays and compared. The results indicated the scale method was reliable, in this population, until the fish reach an age of 5 years. Beyond 5 years there was not close agreement between scale and fin ages. After 8 years, age as determined by scales was invariably less than from fin rays, and sometimes was in error by as much as 5 years.

Received November 27, 1968

INTRODUCTION

In general, fish are "aged" by annual variations in the growth of bony parts, such as scales, spines, bones, or otóliths. For the white sucker, *Catostomus commersoni*, various workers have reported the scales to be satisfactory, unsatisfactory, or of uncertain reliability for age determination. Stewart (1926) described the formation of the annulus in white sucker scales. He had difficulty in determining an annulus beyond the 7th year. His statement, "The rapid growth during the sixth and seventh years seems surprising.", suggests he may have underestimated the ages of the larger fish. Spoor (1939) employed scales for aging white suckers, and was satisfied that an annulus was formed October–May each year, and this annulus could be recognized by crowding of circuli and "cutting over." Raney and Webster (1942), Eddy and Carlander (1942), and Rawson (1951) were able to age suckers by the scale method. Harris (1962) was able to age the related longnose sucker, *Catostomus catostomus*, up to 19 years by scales.

Ovchynnyk (1965) examined the number of ridges in each "year zone" of white sucker scales and noted the variability. As late as September some fish had not added circuli beyond the previous annulus. He concluded, "These observations lead one to be suspicious of the reliability of using year marks on the scales, for age determination in this species." Geen et al. (1966) aged white and longnose suckers by the scales, but noted "returns of marked fish over a number of years indicate that estimates based on scale examination were low." Coble (1967) compared the number of scale annuli on white suckers at tagging and recapture and stated "an annulus was not formed every year."

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During a study of the factors influencing the age and size of white suckers at maturity, the opportunity arose to test the validity of the scale method of aging these fish. Firstly, it was possible to compare the ages of fish obtained from scales and from thin sections cut through the rays of the pectoral fin. In addition, suckers were recaptured in the fall of 1968, a year after these fish had been aged by scale and fin, tagged, and released. This permitted the reexamination of these structures after the fish had spent 1 additional year in its native habitat.

MATERIALS AND METHODS

The study was conducted at George Lake, an oligotrophic lake located at 46°2′N and 81°24′W in the Cloche Mountains of Ontario. The lake has a maximum depth of 39.7 m (130 ft), a mean depth of 18.4 m (60.4 ft), and a surface area of 182 ha (0.702 sq miles). The lake is inhabited by a modest population of rather large suckers.

Two hundred and fifty suckers were sampled in September and October 1967, and data collected on length, weight, sex, and maturity. In addition to a scale sample, the first four pectoral rays were clipped from one fin of each fish. Each fish was tagged with a short length of numbered spaghetti tubing held in place with a loop of monofilament nylon sewn through the musculature under the dorsal fin. Twenty-five fish which had been tagged and sampled previously were recovered in the fall of 1968, and additional scales and fin rays were taken from these fish. The fin-ray method of aging was chosen because it did not require the fish to be killed, as do techniques employing bones.

The method of processing the fins was similar to that described by Scidmore (1953). The pectoral fin, which had been sheared close to the body, was cleaned and air dried. The dry fin was given a thin coat of clear epoxy and permitted to harden. A jeweler's saw with a blade of approximately 33 teeth/cm was used to cut transverse sections close to the base of the rays. Sections were about 0.5 mm thick. In some instances, sections of different thickness and from varying distances from the base of the fin were necessary to determine the number of annuli. The individual sections of ray were mounted in permount and examined under a microscope.

Scales were taken above the lateral line and just posterior to the base of the dorsal fin. Acetate impressions were viewed with a scale projector.

RESULTS

The fin-ray annulus was recognized as an optically less dense zone in transmitted light. The first annulus was complete and new growth was evident by early spring. This first annulus forms close to the center of the ray and could be identified most readily in young fish. (Fig. 1A). In older suckers the first annulus was more difficult to discern from the center of the ray (Fig.1B). Subsequent annuli are easier to interpret in sections of fin rays and counting was routine (Fig. 1A and B).

Of the 250 fish tagged in September 1967, 25 were recaptured in September 1968. The fins of these recaptured fish were examined and an age assigned without reference to the ages given the previous year. The ages of these fish at tagging and on recapture are shown in Table 1. The ages of the recovered fish were from 2 to 12 years when tagged, thus annulus formation could be verified over a range of ages. The rays of two large fish could not be interpreted easily, and in another, the number of annuli was in doubt. With the exception

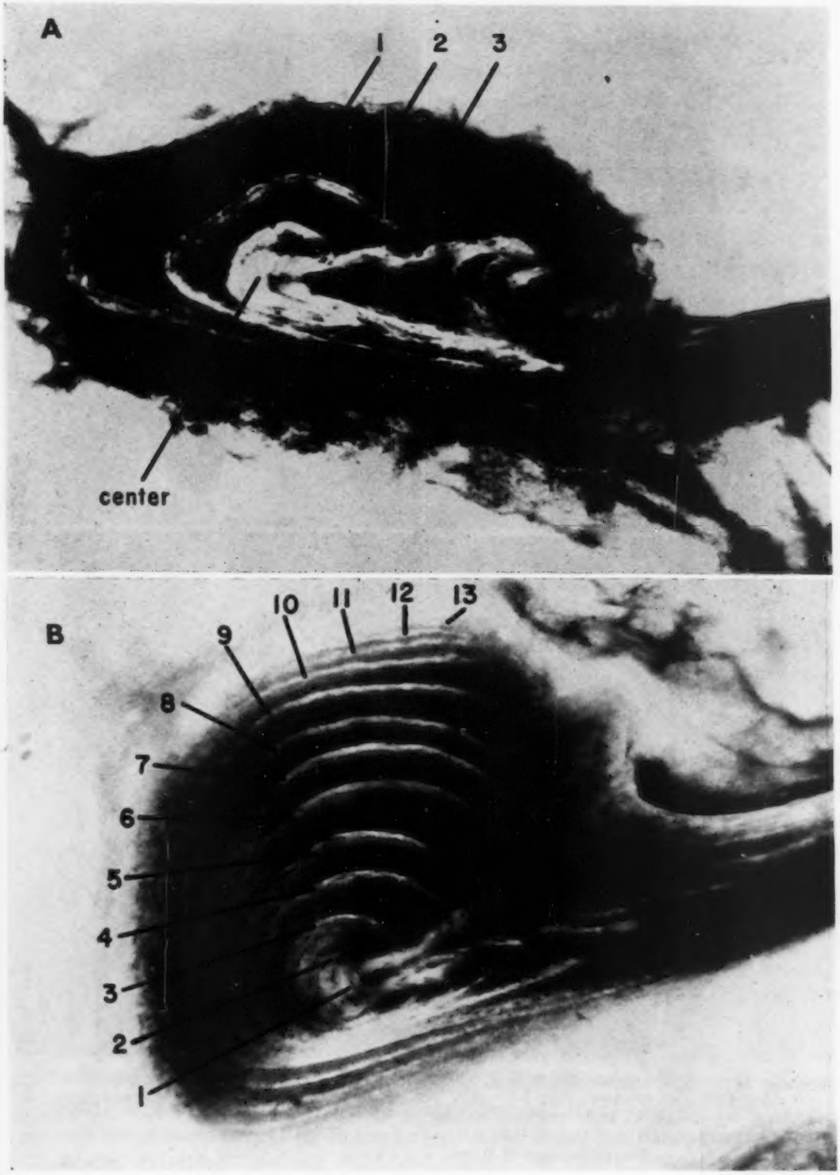
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FIG. 1. Sections of pectoral fin rays of white suckers. A, left pectoral fin of a fish of age 3+ years, with distinct first annulus. B, right pectoral fin of a fish at 13+ years with an indistinct first annulus.

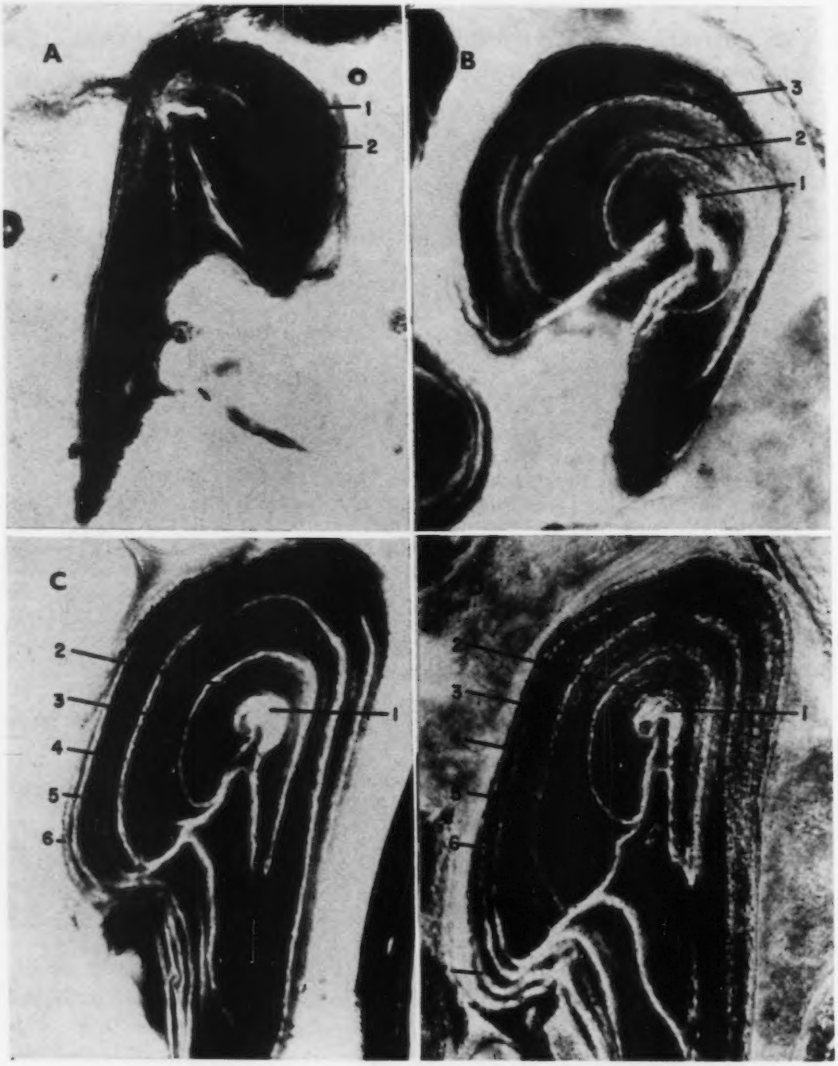

FIG. 2. Sections of pectoral fin rays of white suckers. A, right pectoral of fish no. 5466, taken September 1967 and released. Age 2+ years. B, left pectoral of fish 5466, recaptured September 1968. Age 3+ years. C, right pectoral of fish no. 2390 sampled September 1967 and released. Age 6+ years. D, left pectoral of fish 2390 when recaptured 12 months later. Age 7+ years. Magnifications of A and B are twice that of C and D.

TABLE 1. Fin-ray annuli of fish at marking and on recapture.

Tag no.	Captured, tagged, and fin removed Sept. 1967	Recaptured and second fin removed, Sept. 1968
5479	2+	3+
5466	2+	3+
5497	3+	4+
5313	3+	4+
5404	3+	4+
5499	3+	4+
5500	3+	4+
5495	4+	5+
5488	4+	5+
5291	4+	5+
2265	5+	6+
5465	5+	6+
2051	6+	7+
5397	6+	7+
2390	6+	7+
2299	6+	7+
2037	7+	8+
2231	9+	10+
2043	9+	10+
5432	9+	Too poor to read
2004	10+	11+
2314	11+	12+
2098	11+	Too poor to read
5288	12+	13+
2143	12+	14+ ?

of these three individuals, the recaptured fish showed clearly an additional annulus. The change in the fin-ray section for a 12-month period for fish no. 5466 is illustrated in Fig. 2. The right pectoral fin (Fig. 2A) showed an age of 2+ years in September 1967, and the left pectoral fin (Fig. 2B) an age of 3+ years when the rays of the other fin were removed and examined in September 1968. Similarly, fish no. 2390 was found to be 6+ in September 1967 (Fig. 2C) and 7+ (Fig. 2D) a year later.

Having established the reliability of the fin ray for aging, 157 fish (distinct from those in Table 1) were aged by scales and fin section. Fish that showed no growth beyond the annulus were designated by whole years (e.g. 5 years), and fractional years were indicated (e.g. 5+) where growth of the fin ray and scales extended beyond the annulus.

The relationship between scale age and age from fin rays is illustrated in Fig. 3. The ages are about equal for fish up to 5 years of age. Thereafter scale annuli are less numerous and may read as much as 5 years less beyond age 9. Among fish more than 8 years old the scale age was never equal to the

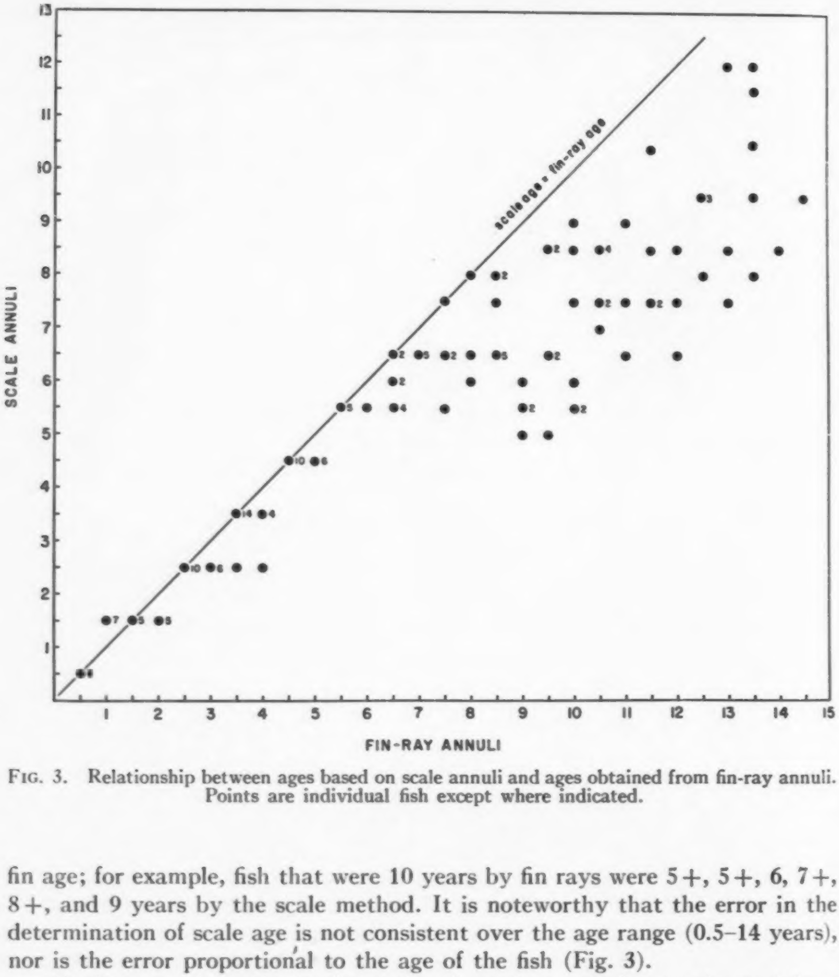

FIG. 3. Relationship between ages based on scale annuli and ages obtained from fin-ray annuli. Points are individual fish except where indicated.

fin age; for example, fish that were 10 years by fin rays were 5+, 5+, 6, 7+, 8+, and 9 years by the scale method. It is noteworthy that the error in the determination of scale age is not consistent over the age range (0.5–14 years), nor is the error proportional to the age of the fish (Fig. 3).

Suckers caught early in the spring showed an annulus on the periphery of the fin sections, but a full annulus was not yet evident on the scales. Thus, in early spring a fish which was 4 years by fin ray was still 3+ years as determined by the scales. In the same fish, by fall, the scales and fin ray both showed the new annulus and new growth, and both would be interpreted as 4+ years. This explains the series of points in Fig. 3, parallel to the theoretical line, "scale age = fin-ray age," but in which the scale age is a fractional year less than the fin-ray age. Of the fish 0–5 years of age, two did not fit this pattern, showing ages of 2+ by scales and 3+ and 4 years on fins.

DISCUSSION

A comparison of ages, obtained by counts of scale and fin-ray annuli, indicates the scale method of age determination is reliable, in this population of white suckers, up to an age of 5 years, with the qualifications expressed above. Beyond 5 years the scale method becomes progressively less reliable. This may explain why some workers have been able to age suckers by means of the scale annuli and others have not. Raney and Webster (1942), for example, were able to age 123 adult suckers between 4 and 7 years. Eddy and Carlander (1942), again using scales, aged 2655 white suckers from 69 lakes and streams; almost all of these fish were 6 years or less. Ovchynnyk (1965) aged 17 white suckers as 4–7 years by scales, but believed these fish were 5–11 years, based on annuli counts on 19 bones. Of this small sample, 13 fish were 6–7 years as interpreted from the scales, and thus the age composition of the 17 fish does not compare with those quoted above. Geen et al. (1966) noted discrepancies between scale age and age based on recapture of marked fish. They believed the scale ages of 6–10 years were low, and suggested many spawners were 10–15 years old.

The results obtained from this population of white suckers in George Lake do not necessarily compromise the ages other workers have obtained for suckers from counts of scale annuli. In populations composed of relatively young fish, the scale age may be the correct age. However, whatever the age composition of a white sucker population, it would seem prudent to verify the scale age by some independent technique, such as bone or fin-ray annuli. Certainly for older white suckers, scales have little value in determining the age of the animal.

ACKNOWLEDGMENTS

This work was supported in part by the Fisheries Research Board of Canada and by the Canadian National Sportsmen's Show, which the authors acknowledge gratefully.

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Corpuscles of Stannius and Renal Physiology in the Eel (*Anguilla rostrata*)

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In freshwater eels there is a significant correlation between glomerular filtration rates (GFR) and urine flow rates suggesting that changes in GFR rather than tubular water reabsorption lead to the major adjustments in urine flow rates accompanying changes in environmental salinity.

Removal of the corpuscles of Stannius was not followed by a significant change in GFR indicating that an adequate (normal) effective filtration pressure is independent of a corpuscular pressor substance.

In 8 of 17 Stanniectomised eels urine flow rates exceeded GFR demonstrating that, under these experimental conditions, eel renal tubules secrete water.

Multiple tissue electrolyte changes followed Stanniectomy; the 75% increase in the plasma calcium concentration is of particular interest. This increase was probably due to a reduction in the net rate of calcium deposition in bone and not to a change in the renal handling of calcium.

Received December 2, 1968

INTRODUCTION

Two corpuscles of Stannius (Stannius, 1839) are lodged in the mesonephric kidney of the majority of bony fishes although the number tends to be greater in the more primitive forms. *Amia calva*, for example, possesses between 40 and 50 corpuscles (Garrett, 1942; Bauchot, 1953).

Teleostean corpuscles were once thought to be homologous to the adrenal cortical tissue of higher vertebrates. It has since been shown that they develop as protrusions from the pro- and mesonephric ducts (Huot, 1898; Giacomini, 1933; Ford, 1959; De Smet, 1962), whereas adrenocortical (interrenal) tissue is derived from coelomic epithelium (Giacomini, 1933). In most bony fishes, with the exception of those in the class Acipenseridae, islets of cortical cells are located in the anterior head kidney and in or against the walls of the cardinal veins (see reviews by Van Overbeeke, 1960; Nandi, 1962).

In the Japanese eel (*Anguilla japonica*) the corpuscles of Stannius constitute a number of ovoid and polymorphic lobules consisting of radially orientated columnar secretory cells (Fujita and Honma, 1967). Each secretory cell is characterised by numerous round cytoplasmic granules and rough-surfaced endoplasmic reticulum, the overall appearance resembling that of a cell from the exocrine pancreas (Palade, 1956; Ristow and Piepho, 1963). The fine structure of North American eel (*Anguilla rostrata* LeSueur) corpuscles is similar (D.G. Butler and H. Harvey, unpublished data). Adrenocortical cells

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are characterised by a smooth endoplasmic reticulum, lipid droplets, and mitochondria with tubular crests (Rhodin, 1963). Earlier studies with the light microscope demonstrated that European eel (*Anguilla anguilla* L.) corpuscular cells are sudanophilic (Bodin, 1949; Ogawa, 1963) and contain ascorbic acid (Fontaine and Hatey, 1953): both staining properties are considered to be typical of adrenocortical tissue. Nevertheless, Chieffi and Botte (1963) failed to demonstrate histochemically steroid-3*β-ol*-dehydrogenase in corpuscles from the same species.

Attempts have been made to extract adrenocortical steroids from corpuscles of Stannius. Extracts from 10 g of Atlantic salmon (*Salmo salar*) corpuscles were reported to contain cortisol and corticosterone (Fontaine and Leloup-Hatey, 1959). Ford (1959) extracted methanol-preserved sockeye salmon (*Oncorhychus nerka*) corpuscles, but failed to detect steroids of the C_{21} type. Incubated corpuscular tissue from several teleost species has failed to convert labelled substrate to steroids (Ford, 1959; Phillips and Mulrow, 1959; Chester Jones et al., 1965), although Idler and Freeman (1966) have reported the limited in vitro conversion of 4-C^{14} progesterone to 11-deoxycorticosterone by the corpuscles of the Atlantic cod (*Gadus morhua*).

Chester Jones et al. (1966) reported that corpuscles of Stannius of the European eel contain an extractable pressor substance with some of the biochemical properties characteristic of mammalian renin. When injected intravenously to freshwater silver eels, saline extracts of the corpuscles produced a significant and prolonged increase in pneumogastric arterial pressure. After removal of the corpuscles, pneumogastric arterial pressure fell to the level recorded for eels adapted to sea water. This raised the possibility that, in freshwater eels, a release of the pressor substance could lead to an increase in the effective filtration pressure and consequently the rate of urine flow (Sharrat et al., 1964; Chester Jones et al., 1966; Rankin, MS, 1967). A decrease in its synthesis and release might partially account for the sharp reduction in glomerular filtration rates (GFR) and urine volume in eels adapted to sea water (Sharrat et al., 1964; Rankin, MS, 1967).

In the present experiments kidney function and tissue electrolyte concentrations were measured in order to learn more about the role of corpuscular secretions in kidney function and salt-electrolyte balance in freshwater North American eels.

MATERIALS AND METHODS

Fish

Mature (silver) female North American eels (*A. rostrata* LeSueur) were collected from the St. Lawrence River near Quebec City in October 1967 and transported to the Department of Zoology. They were held in aquaria supplied with running dechlorinated tap water (10 C), starved, and acclimated for at least 3 weeks before they were used for experiments.

Removal of the Corpuscles of Stannius

Eels were anaesthetised in an M.S. 222 solution (0.4 g/liter) and placed ventral side uppermost on a bench covered with wet towelling. A 3-inch incision through the body wall was made parallel to and ¼ inch below the lateral line at the level of the cloaca. Edges of the body wall were retracted so that the urinary bladder could be lifted free of the kidney to expose the paired corpuscles embedded in its midventral surface. The corpuscles were freed of adhering tissue and removed. Bleeding was minimal and there was no apparent damage to a series of ureters which drain the kidney and lead to the urinary bladder. The bladder was returned to its original position and the wound sutured with stainless steel wire. Sham-operated eels were treated similarly but the corpuscles were not removed.

Groups for Creatinine Secretion and Clearance Experiments

Single urine samples were collected from a group of 10 freshwater silver eels and were tested for the presence of endogenous creatinine using the methods given below. A second group of 10 eels from the same stock were injected intraperitoneally with 5.0 ml per kg body weight of an aqueous 5.76% creatinine – 5.0% inulin solution. Plasma and urine creatinine and inulin concentrations were determined. Together with urine flow rates these data were then used to calculate creatinine and inulin clearance rates.

Groups for Stanniectomy Experiment

Eels were separated into three experimental groups: intact control eels, sham-operated eels, and Stanniectomised eels. Three weeks after the operations were performed, inulin clearance and urine flow rates together with urinary, plasma, and muscle electrolyte concentrations were determined for eels in each of the three groups. These data were used to calculate the percentage renal tubular reabsorption of water and electrolytes and the net rates of excretion for certain ions (Tables 1–5).

Urine Collection and Calculation of the Glomerular Filtration Rate

Eels were lightly anaesthetised in an aqueous M.S. 222 solution (0.4 g/liter). A ½-inch length of Intramedic (PE240) polythene tubing was inserted through the urinary papilla into the urinary bladder and tied firmly in place with a cloacal purse-string ligature. The catheterised eel was injected intraperitoneally with 5.0 ml per kg body weight of either an aqueous 5.76% creatinine – 5.0% inulin solution or with the same volume of a 5.0% inulin solution in isotonic saline. The latter solution was used for all experiments except the preliminary one designed to show whether or not endogenous and exogenous creatinine or both is secreted by the eel kidney.

Each eel was replaced in fresh water where it remained, undisturbed, for 18 hr. At the end of this period the eel was removed from the aquarium, gently wrapped in a wet towel, and placed ventral side upwards. If handled carefully in this way, the unanaesthetised fish did not struggle and lay motionless for as long as 15 min. During this time a finger cot (London Rubber Industries) was washed with glass distilled water, deflated, and tied over the end of the protruding catheter. Dead space was minimal. The eel was then returned to the aquarium for a 5-hr urine collection terminated by the removal of the urine sample from the finger cot. Eels were then anaesthetised and a blood sample was withdrawn from the heart with a 10-ml heparinised Vacutainer (Becton-Dickinson, Toronto) fitted with an #18 gauge hypodermic needle. Epaxial muscle was excised, weighed, and processed for ion analysis (Butler and Langford, 1967).

In the present experiments plasma concentrations of both inulin and creatinine became uniform within 10 hr after they were injected and slowly decreased thereafter. The half-life for the plasma inulin concentration in other teleost fishes, depending upon species and the route of injection, ranges from 30 to 300 hr (Holmes and McBean, 1963; Maetz et al., 1964a; Holmes and Stainer, 1966; Rankin, MS, 1967; Hickman, 1968). The inulin concentration in each terminal plasma sample was therefore assumed to be almost equal to what it had been 5 hr earlier.

Plasma and urine inulin concentrations were measured using the direct resorcinol method without alkali treatment (Schreiner, 1950). Creatinine was measured using the method of Jaffé (1886) as modified by Brod and Sirota (1948). Inulin and creatinine clearance rates were then calculated according to Smith (1956).

Tissue Electrolyte Concentrations

Plasma and urine samples were suitably diluted for ion analysis. Sodium and potassium concentrations were then measured with a Zeiss PF 5 flame photometer. Chloride concentrations were determined with a Buchler–Cotlove chloridometer. Plasma and urinary calcium concentrations were measured by flame emission at 422.7 mμ using a Zeiss PMQ 11 spectrophotometer equipped with a double monochromator and flame attachment. Magnesium concentrations were measured with the same instrument employing atomic absorption using a hollow cathode lamp (285.2 mμ). Muscle electrolyte concentrations were measured in 10% trichloroacetic acid extracts of dried, fat-free samples according to the procedure given by Butler and Langford (1967).

RESULTS

TUBULAR SECRETION OF CREATININE BY THE KIDNEY OF FRESHWATER SILVER EELS

The creatinine/inulin excretion ratio was 1.28 for freshwater silver eels indicating that, assuming inulin is inert, exogenous (injected) creatinine was secreted by the eel kidney. For this reason all further determinations of GFR were based on inulin clearance. Creatinine was not detected in any of 10 urine samples collected from intact freshwater eels.

GLOMERULAR FILTRATION RATES, URINE FLOW RATES, AND TUBULAR SECRETION OF WATER

Figure 1 shows that in intact, sham-operated and Stanniectomised freshwater silver eels there is a statistically significant ($P < 0.05$) correlation between the GFR and the rate of urine flow.

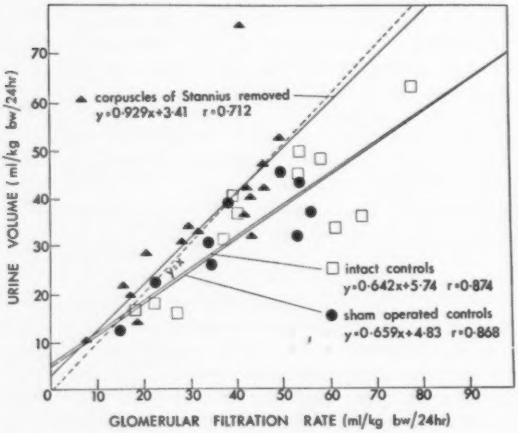

FIG. 1. Correlation between urine flow rates and glomerular filtration rates in intact, sham-operated, and Stanniectomised freshwater silver eels.

Freshwater silver eels do not depend upon a corpuscular pressor substance for a normal effective renal filtration pressure. Table 2 shows that after Stanniectomy the mean GFR decreased from 38.0 ± 4.8 to 32.5 ± 3.3 ml/kg body weight per 24 hr, whereas the mean urine flow rate increased from 29.9 ± 3.6 to 32.4 ± 2.9 ml/kg body weight per 24 hr. Neither of these changes is statistically significant ($P = 0.05$).

If individual GFR's are plotted against individual urine flow rates (Fig. 1) in each experimental group, the slope of the linear regression for Stanniectomised eels is significantly different (Steel and Torrie, 1960) from that for the sham-operated controls ($P < 0.05 > 0.01$). Thus, in Stanniectomised eels the urine flow rate tends to equal the GFR and, in 8 out of 17 eels, exceeds it. Table 3 shows that the mean percentage tubular reabsorption of water is 22.8 ± 4.6% for intact eels, 19.9 ± 4.4% for sham-operated eels, and -5.7 ± 8.4% for Stanniectomised eels. Provided there was no trans-tubular flux of inulin, the results demonstrate clearly that under these conditions, the eel renal tubule is capable of secreting water.

PLASMA AND URINE ELECTROLYTE CONCENTRATIONS

Plasma sodium, chloride, and magnesium concentrations decreased after Stanniectomy whereas plasma potassium and calcium concentrations increased (Table 1).

Urinary sodium and chloride concentrations decreased significantly (Table 1), but the percentage tubular reabsorption of these ions did not change (Table 3). Urinary potassium and calcium concentrations increased although there was a decreased net tubular reabsorption of these ions. Both plasma and urine osmolarities decreased significantly (Table 1).

URINARY EXCRETION OF SOLUTES

Table 4 shows that excretion rates (μeq/kg body weight per 24 hr) for some solutes changed after Stanniectomy. Renal sodium excretion decreased significantly; however the excretion of chloride only tended to decrease. Calcium excretion increased three-fold. Rates of potassium, magnesium, and total solute excretion were the same as for sham-operated controls.

MUSCLE ELECTROLYTES

Epaxial muscle sodium and chloride concentrations decreased significantly after removal of the corpuscles, but muscle potassium did not change (Table 5). Water in whole or fat-free muscle did not change after Stanniectomy, but did increase in sham-operated eels as compared with intact eels.

DISCUSSION

Creatinine was not detected in any of 10 urine samples from freshwater silver eels although Smith (1929) had earlier reported the presence of this compound (0.1–2.0 mg/100 ml) in urine samples collected from freshwater eels of the same species. This negative finding did not exclude the possibility that eel renal tubules could secrete exogenous creatinine, in which case, creatinine clearance measurements would be of little value for determining the glomerular filtration rate. The experiment based on the intraperitoneal injection of a 5.76% creatinine – 5.0% inulin solution followed by the measurement

TABLE 1. Urine and plasma electrolyte and osmotic concentrations in freshwater silver eels (*Anguilla rostrata*) after removal of the corpuscles of Stannius.[a]

Group	*n*	Plasma (*meq/liter*)					Milliosmols/litre	Urine (*meq/liter*)					Milliosmols/litre
		Na	K	Cl	Ca	Mg		Na	K	Cl	Ca	Mg	
Intact controls	14	141.4 ±3.6	1.92 ±0.12	104.5 ±3.00	5.27 ±0.29	2.19 ±0.14	295.7 ±5.1	18.20 ±1.70	0.68 ±0.10	8.40 ±1.10	2.01 ±0.21	0.522 ±0.090	49.20 ±2.52
Sham operated	10	148.1 ±1.6	2.22 ±0.11	99.21 ±2.72	7.13 ±0.44[b]	3.46 ±0.22[b]	313.8 ±3.5	19.83 ±2.76	0.35 ±0.05	10.63 ±2.33	2.98 ±0.27	0.560 ±0.082	57.16 ±3.52
Corpuscles removed	18	136.8 ±2.0	3.49 ±0.32[b,c]	80.26 ±3.20[b,c]	12.33 ±1.35[b,c]	2.28 ±0.20[c]	291.6 ±5.5[c]	11.92 ±1.39[b,c]	0.59 ±0.15	6.46 ±0.86	6.69 ±0.86[b,c]	0.620 ±0.091	43.98 ±3.07[b,c]

[a] Values are means ± SE. Multiple comparisons of means in each experimental group were made using Tukey's *w*-procedure (Steel and Torrie, 1960).

[b] $P < 0.05$ compared with intact controls.

[c] $P < 0.05$ compared with sham-operated controls.

TABLE 2. Body weights, glomerular filtration rates (GFR), and urine flow rates in freshwater silver eels (*Anguilla rostrata*) after removal of the corpuscles of Stannius.[a]

Group	*n*	Body wt (*g*)	GFR (*ml/kg body wt per 24 hr*)	Urine volume (*ml/kg body wt per 24 hr*)
Intact controls	14	1153.1±78.6	46.9±5.4	34.7±3.9
Sham operated	10	990.0±125.5	38.0±4.8	29.9±3.6
Corpuscles removed	18	1134.4±86.0	32.5±3.3	32.4±2.9

[a] Values are means ± SE. Multiple comparisons of means in each experimental group were made using Tukey's *w*-procedure (Steel and Torrie, 1960) but there were no significant differences ($P = 0.05$).

of the simultaneous excretion of both compounds clearly showed that exogenous creatinine is secreted by the kidney tubules.

RELATIONSHIP BETWEEN GFR AND URINE FLOW RATES

Figure 1 shows that there is a highly significant correlation between the glomerular filtration rates and urine flow rates in each of the three experimental groups: intact control, sham-operated, and Stanniectomised freshwater silver eels. Sharratt et al. (1964) suggested that urine flow rates in freshwater European eels (*A. anguilla* L.) are related to changes in GFR, but Rankin (MS, 1967) first clearly demonstrated a significant correlation between these two parameters in European eels adapted to fresh and sea water. A similar correlation has been demonstrated in, or suggested for, other teleost species (Holmes and McBean, 1963; Maetz et al., 1964b; Stanley and Fleming, 1964; Holmes and Stainer, 1966; Hickman, 1968).

In Stanniectomised freshwater North American eels the correlation between urine flow rates and GFR was significant, but the regression line shifted away from those for intact and sham-operated eels toward $y = x$. In at least 8 of 17 eels the urine flow rate exceeded the plasma filtration rate indicating that the tubules can both reabsorb and secrete water in the process of forming urine, the interplay between the two processes determining its final concentration. This finding is in agreement with that of Rankin (MS, 1967) who observed renal tubular secretion of water in Stanniectomised freshwater yellow *A. anguilla*. Table 3 shows that the net tubular reabsorption of water was 19.9 ± 4.4% for sham-operated animals and −5.7 ± 8.4% after removal of the corpuscles of Stannius. It is therefore possible that some compound, secreted by the corpuscles, normally regulated the tubular permeability to water derived from the peri-tubular fluids and transported into the lumen by some process such as local osmosis (Diamond and Tormey, 1966). The changes observed after removal of the corpuscles suggest that this compound decreases permeability of the tubules.

TABLE 3. Per cent tubular reabsorption of water and solutes in freshwater silver eels (*Anguilla rostrata*) after removal of the corpuscles of Stannius.[a]

Group	*n*	Water	Na	K	Cl	Ca	Mg	Milliosmols
Intact controls	14	22.8 ±4.6	89.23 ±1.56	69.80 ±4.00	93.40 ±0.77	72.06 ±3.02	81.46 ±4.96	85.50 ±1.01
Sham operated	10	19.9 ±4.4	88.76 ±3.68	86.62 ±2.02[b]	91.99 ±1.54	65.52 ±3.83	86.92 ±2.17	85.00 ±1.22
Corpuscles removed	18	−5.7 ±8.4[b,c]	82.18 ±4.70	74.11 ±5.95	88.16 ±3.38	58.45 ±5.30	70.87 ±6.91	84.38 ±3.04

[a] Values are means ± SE. Multiple comparisons of means in each experimental group were made using Tukey's *w*-procedure (Steel and Torrie, 1960).

[b] $P < 0.05$ compared with intact controls.

[c] $P < 0.05$ compared with sham-operated controls.

TABLE 4. Rate of solute excretion by freshwater silver eels (*Anguilla rostrata*) after removal of the corpuscles of Stannius.[a]

Group	*n*	μeq/kg body wt per 24 hr					Milliosmols
		Na	K	Cl	Ca	Mg	
Intact controls	14	677.7 ±119.5	15.50 ±8.34	308.7 ±60.7	66.01 ±8.30	15.27 ±1.28	1918.1 ±257.6
Sham operated	10	576.5 ±100.3	10.61 ±2.28	291.3 ±56.6	87.33 ±11.40	14.67 ±1.35	1396.5 ±306.4
Corpuscles removed	18	390.4 ±34.1[b,c]	16.48 ±3.09	233.3 ±22.4	249.02 ±42.89[b,c]	19.39 ±5.10	1734.9 ±135.8

[a] Values are means ± SE. Multiple comparisons of means in each experimental group were made using Tukey's *w*-procedure (Steel and Torrie, 1960).

[b] $P < 0.05$ compared with intact controls.

[c] $P < 0.05$ compared with sham-operated controls.

TABLE 5. Electrolyte concentrations in freshwater silver eel (*Anguilla rostrata*) epaxial muscle after the removal of the corpuscles of Stannius.[a]

		meq/kg muscle water			meq/kg fat-free wet muscle				
Group	*n*	Na	K	Cl	Na	K	Cl	% muscle water	% fat-free muscle water
Intact	14	27.79	154.5	16.24	19.88	117.1	11.66	53.04	71.74
control		±0.64	±4.36	±0.51	±0.67	±3.43	±0.39	±1.02	±1.05
Sham	10	29.11	147.3	12.54	22.05	111.4	9.50	61.85	75.62
operated		±1.03	±2.97	±0.28[b]	±0.87	±2.39	±0.19[b]	±1.22[b]	±0.66[b]
Corpuscles	18	22.44	140.2	10.77	17.22	106.6	7.86	60.39	76.08
removed		±1.40[b,c]	±4.62	±0.54[b]	±0.99[c]	±3.24	±0.38[b]	±0.80[b]	±0.29[b]

[a] Values are means ± SE. Multiple comparisons of means in each experimental group were made using Tukey's *w*-procedure (Steel and Torrie 1960).

[b] $P < 0.05$ compared with intact controls. [c] $P < 0.05$ compared with sham-operated controls.

In the aglomerular kidney, urine is formed by the tubular secretion of water and solutes rather than by glomerular filtration, followed by the transtubular flux of both (Marshall, 1930; Bieter, 1931; Marshall and Grafflin, 1932; Brull and Nizet, 1953; Forster, 1953; Forster and Berglund, 1953). Tubular secretion does not occur only in aglomerular kidneys. When the marine sculpin (*Myoxocephalus octodecimispinosus*) is injected with phloridzin, its glomerular kidney becomes functionally aglomerular: water and solutes such as sulphate and magnesium are secreted by the proximal convolution whereas chloride is both secreted and reabsorbed (Marshall and Grafflin, 1932). The marine sculpin is ideal for such studies because the kidney tubules lack not only a loop of Henle but also a distal convolution. The movement of both solutes and water must therefore occur in the proximal convolution. The present observations and those of Marshall and Grafflin (1932) raise the possibility that the bi-directional flux of water and electrolytes occurs in other fully glomerular teleost kidneys. Provided urine flow was always less than the GFR the tubular secretion of ions and water would not be detected.

European eel corpuscles of Stannius contain an extractable pressor material with some, but not all, of the biochemical properties characteristic of mammalian renin (Chester Jones et al., 1966). After Stanniectomy, pneumogastric arterial pressure, normally 26.3 ± 2.0 mm Hg in freshwater eels, decreased to 17.5 ± 1.5 mm Hg, the latter pressure being about the same as that for seawater-adapted eels. It was then inferred that a corpuscular pressor substance, by modifying eel blood pressure could in part regulate changes in the GFR and hence the rate of urine flow during adaptation to either fresh or sea water. My findings are not in agreement with this hypothesis. Before Stanniectomy the GFR in freshwater *A. rostrata* was 38.0 ± 4.8 ml/kg body weight per 24 hr and afterward 32.5 ± 3.3 ml/kg body weight per 24 hr. As this difference is not significant the corpuscles probably have little if any control over GFR during adaptation to changes in environmental salinity. Moreover, changes in pneumogastric arterial pressure may bear little relationship to either renal arterial pressure or effective renal plasma flow.

Even though it is tempting to assign some physiological role to the extractable pressor material from freshwater eel corpuscles of Stannius, the following points must be considered: (*a*) juxta-glomerular (JG) cells, believed to be a source of mammalian renin (Cook and Pickering, 1958; Pitcock et al., 1959; Edelman and Hartroft, 1961; Hartroft et al., 1964) have been located in the eel kidney, but not in the corpuscles of Stannius (Capréol and Sutherland, 1968); (*b*) the corpuscular pressor substance has fewer of the biochemical–physiological characteristics of standard pig renin than the kidney pressor substance from the same eel (Chester Jones et al., 1966; Sokabe et al., 1966; Mizogami et al., 1968); (*c*) eel kidney extracts incubated with ox serum substrate yield an angiotensin-like pressor substance whereas corpuscular extracts do not (Chester Jones et al,. 1966); (*d*) since eel kidneys produce renin, the need for another smaller source of a renin-like material is questionable.

Finally, in view of the repeated failure to detect aldosterone in eel interrenal incubates (Butler, 1965; Leloup-Hatey, 1965; Sandor et al., 1966) it is unwise to postulate a renin–angiotensin–aldosterone system in eels, regardless of the site of renin production.

Further experiments may clearly show that a corpuscular pressor substance normally increases renal arterial blood pressure, but does not reduce the glomerular filtration rate by afferent arteriolar constriction as is often the case after the intravenous injection of angiotensin in man (Brown, 1963; Peart, 1965). Compensatory changes in regional blood flow might therefore mask the effect of Stanniectomy and give rise to the changes in renal physiology observed in the present experiments. These changes could include an increase in renal portal blood flow leading to an increased effective filtration rate and a greater circulation to the peritubular capillary network. The latter change could then directly augment the tubular secretion of ions and water (Tables 1-5). One could normally test part of this hypothesis by measuring not only inulin clearance (GFR) but also para-aminohippuric acid clearance (effective renal plasma flow). However the caudal venous circulation in eels is so arranged that data for PAH clearance would have little meaning (see Mott, 1950; Hickman, 1965; Rankin, MS, 1967).

Effect of Stanniectomy on Calcium and Magnesium Metabolism in Freshwater Eels

Rasquin (1956) showed that teleostean corpuscles of Stannius may be important for hydro-mineral regulation. When KCl solution was injected into *Astyanax mexicanus* or if intact fish were placed in 1% saline, corpuscular cells decreased in size and activity. However, if the fish were placed in distilled water, the cells hypertrophied. Two years later Vargas and Concha (1957) further implicated the corpuscles in electrolyte balance by reporting that Stanniectomy of *Sicyases sanguineas* was followed by plasma sodium depletion. European eels were first Stanniectomised by Vincent who referred to the corpuscles as the suprarenal bodies (Vincent, 1898) and later by Fontaine (1964) who reported that Stanniectomy was followed by changes in serum sodium, potassium, and calcium concentrations. Serum calcium in these eels increased by 141% but returned to normal after the intra-muscular injection of a brei of lyophilised corpuscles, as did the elevated potassium concentrations and decreased sodium and phosphate concentrations.

Urinary calcium concentrations in North American eels increased after Stanniectomy as did the net rate of calcium excretion (Tables 1 and 3). These changes were not due to a decrease in the percentage reabsorption of calcium nor to a change in the GFR but solely due to a marked increase in plasma calcium concentrations (Tables 1–3).

Moss (1961) states that, in teleosts including the eel, bone is acellular and therefore available for calcium deposition but not reabsorption. Others (Rosenthal, 1963; Urist, 1966) suggest that calcium can be slowly withdrawn from acellular bone and therefore is involved in ion homeostasis. In agreement with the latter hypothesis, Fleming (1967) has suggested that as inorganic phosphate is present in low concentration in fresh water, the important role of acellular bone may be to provide a ready source of phosphate rather than calcium. Fontaine's (1967) data showing that Stanniectomy is followed by a lowered serum phosphate, raises the possibility that eel corpuscles normally secrete a substance which accelerates calcium deposition in bone and releases phosphate into the circulation.

After Stanniectomy, plasma magnesium concentrations decreased but urinary magnesium concentrations did not change significantly (Table 1), indicating that the tubular reabsorption of magnesium decreased or secretion increased or both. The urine flow rate did not change substantially; therefore the net rate of magnesium excretion was the same as for sham-operated controls. In contrast, Chan et al. (1967) measured serum magnesium in intact and Stanniectomised freshwater European eels and found no measurable difference in concentration.

CHANGES IN URINARY AND PLASMA SODIUM, POTASSIUM, AND CHLORIDE CONCENTRATIONS AFTER REMOVAL OF THE CORPUSCLES OF STANNIUS

The statistically significant reduction in plasma sodium (7.6%) and chloride (19.2%) and increase in potassium (36.6%) closely parallels the changes reported to follow Stanniectomy in freshwater European eels, *A. anguilla.* (Fontaine, 1964; Leloup-Hatey, 1964a, b; Chan et al., 1967).

Urinary sodium and chloride concentrations in Stanniectomised eels decreased by 40 and 39% respectively compared with operated controls, yet only the rate of net sodium excretion decreased significantly (Table 4). It follows that the branchial net influx rates for both sodium and chloride are directly or indirectly reduced due to Stanniectomy. Neither the urinary potassium concentration nor the rate of potassium excretion changed significantly after Stanniectomy. Therefore the increased plasma potassium concentration probably represents a slight shift of this ion, out of muscle cells, into the extra-cellular fluid.

CHANGES IN MUSCLE ELECTROLYTE CONCENTRATIONS AFTER REMOVAL OF THE CORPUSCLES OF STANNIUS

Table 5 shows that Stanniectomy was followed by a decrease in eel muscle sodium concentration and content although muscle chloride and potassium concentrations did not change significantly. The sham operation produced not only an increase in muscle water, but also a decrease in muscle chloride similar to that after sham-adrenalectomy (Butler et al., 1969). Muscle electrolyte data for Stanniectomised eels were compared with data for intact control eels in the experiments of Chan et al. (1967) and Leloup-Hatey (1964a, b). Their data should therefore be re-evaluated.

Changes in ionic composition of eel plasma and muscle after removal of the corpuscles of Stannius have little in common with those which typify surgical adrenalectomy (Butler and Langford, 1967; Chan et al., 1967; Butler et al., 1969). The marked increase in eel plasma calcium and reduction in plasma chloride observed in the present experiments have not been observed in adrenalectomised eels (*Anguilla* spp). Moreover, in eels, adrenalectomy was followed by a loss of muscle potassium whereas in the present experiments and those of Leloup-Hatey (1964a, b) muscle potassium did not change and plasma potassium levels increased significantly. The only electrolyte changes common to both operations were the decreased plasma and muscle sodium concentrations.

ACKNOWLEDGMENTS

This research was supported by operating grants from the Fisheries Research Board and National Research Council of Canada to the author. Dr I. Radde, Department of Paediatrics, The Hospital for Sick Children, Toronto, Ont., kindly measured calcium and magnesium concentrations in plasma and urine samples.

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Variance Components in the Estimation of Potential Egg Deposition of Sockeye Salmon Escapements[1]

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MATHISEN, OLE A., AND TOR GUNNERØD. 1969. *Variance components in the estimation of potential egg deposition of sockeye salmon escapements.* J. Fish. Res. Bd. Canada 26: 655–670.

The magnitude of the variance components in the estimation of the potential egg deposition of sockeye salmon escapements to the Kvichak District, Bristol Bay, Alaska, was determined from data collected from 1957 to 1966. The greatest variance component was caused by estimation of the escapement followed by the variance due to estimation of the ratio of females in the escapement. Estimation of the average fecundity added the least variance.

Received August 12, 1968

INTRODUCTION

SINCE 1955, the sockeye salmon escapement to the Kvichak River system, which drains into Bristol Bay, Alaska, has been estimated annually. The run has exhibited a cyclic variation in abundance, and the cycle has been of 4 or 5 years' duration. The estimated escapements have ranged from 251,000 to 24.3 million spawners. In spite of this tremendous range, it has not been possible to establish a well-defined relationship between numbers of spawners and those of returns according to the general formulation of Ricker (1954). Although large escapements have produced large returns and small escapements small returns, there has been considerable variability in the return per spawner, especially for escapements between 250,000 and 700,000 spawners. Errors in assessing the size of the escapement as a measure of reproductive potential hinges on a constant sex ratio and a constant fecundity. Usually this condition is not met. Therefore Paulik and Greenough (1966) have suggested that either the number of females in the escapement or the potential egg deposition should be used as a measure of the reproductive potential and serve as the independent variable in spawner-recruit relationships. Undoubtedly, the suggestion merits serious consideration in the case of the salmon escapement to the Kvichak River system, as well as other stream escapements in the Bristol Bay area, since the instantaneous fishing rate of gillnets in the fishery is higher for males than females and at times results in a rather high percentage of females in the escapement.

Furthermore, the Bristol Bay sockeye runs consist primarily of two size groups of fish, those fish that spend 2 years in the sea, or 2-ocean fish, and

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Printed in Canada

those that return after 3 years in the sea, or 3-ocean fish. Each of these groups spend either 1 or 2 years in fresh water. Thus, the run is made up largely of four year-classes, 4_2, 5_2, 5_3, and 6_3. Since fecundity is a function of size or its equivalent ocean age, the potential egg deposition is greatly influenced by the ratio of 2- and 3-ocean females in the escapement.

The purpose of this paper is to estimate the relative magnitudes of the major sources of variation in the estimation of the reproductive potential of escapements to the Kvichak River system.

ESTIMATORS OF POTENTIAL EGG DEPOSITION

The number of eggs available for deposition (PE) from an escapement can be computed as the product of the total number of fish in the escapement (N), the sex ratio as the fraction of females (P), and the average number of eggs per female ($\bar{F}$). Hence:

$$PE = N \cdot P \cdot \bar{F} \qquad (1).$$

If there exists a linear relationship between the lengths of females and the numbers of eggs produced, the average number of eggs produced by females of average length (F) could be substituted for $\bar{F}$.

When the number of females is used in spawner-recruit relationships, the assumption is made that the potential egg deposition is proportional to the number of females, i.e., they are all of constant fecundity. When the total escapement is used as the independent variable, the underlying assumption is that the potential egg deposition is proportional to the numerical size of the escapement, which is of fixed sex ratio and fecundity.

N, P, and $\bar{F}$ can be considered to be independent, so that the variance of PE can be approximated by

$$\hat{Var}\ PE = PE^2 \left[\frac{\hat{Var}\ N}{N^2} + \frac{\hat{Var}\ P}{P^2} + \frac{\hat{Var}\ \bar{F}}{\bar{F}^2} \right] \qquad (2).$$

ESTIMATION OF THE ESCAPEMENT

The size, sex ratio, and length frequency distribution of the annual escapement to the Kvichak River are determined at Igiugig near the outlet of Iliamna Lake.

The size of the escapement is estimated by a 10-min sample count, which is started at the same time every hour from towers erected near the banks of the stream (Becker, 1962). Counting commences when the first ascending salmon appear and continues day and night until only a few hundred fish pass each day.

For the 3 years under consideration, 1964, 1965, and 1966, 10-min hourly counts were made from the left and right bank of the main stream and in a side branch where counting followed a less rigid schedule, but always when fish were passing. It has been assumed that a no-count in the side branch corresponds to a zero count. This is a minor assumption since the counting crew was stationed at this branch and observed hourly, to see if fish were ascending the branch of the stream, on their way to the main stream towers.

Counting commenced at hourly fixed times. Since the migration of fish within an hour can be assumed to be randomly distributed in relation to the fixed starting of the count, the 10-min counts have been treated as if they were made randomly within the hour. The estimate of the total escapement is then the sum of seasonal daily hourly estimates. Consequently,

$$\hat{N} = 6 \sum_{i=1}^{n} \sum_{j=1}^{24} x_{ij} \tag{3}$$

where $\hat{N}$ is the estimate of the total escapement, n is the number of counting days, and x_{ij} the sum of the three hourly 10-min counts. The counting scheme is a complete factorial experiment with days and hours as fixed factors and hourly counts as a random one.

The accuracy of the 10-min counts is influenced by variable visibility at the tower sites, by personal bias introduced by the use of different observers, and by counting by larger units — 5, 10, or even 100 fish — during heavy migration. Thus, the variance of the total estimate is influenced only by the variance of the hourly counts and the variance of the observers. Unfortunately, neither of these sources of variability have been investigated by repeated and duplicated counts within the hour.

Seibel (1967) has given an estimate of the mean relative error of the 10-min counts expanded to 1 hr by multiplication with the factor 6 in relation to complete hourly counts, assuming that the counts were randomly chosen without error and omitting the effects of tower sites and days. He concludes that the relative error is less than 10%.

Another measure of the hourly variability is afforded by considering all the 24 counts made daily through the season as parts of 24 systematic samples. For each set a mean $\bar{x}_{sy}$ can be computed and the variance between these means ascertained. This variance is then an estimate of the variance associated with the mean seasonal count (Table 1).

If the migration rate of fish was randomly distributed within all hours of the day, this variance estimate should be reduced substantially in relation to the variance estimate obtained by taking each count as representative of all possible counts. In reality, the achieved reduction in variance was rather minor because the migration of fish follows a daily pattern with a lower migration rate during hours of darkness. The variance estimates used in Table 1 are therefore inflated estimates of the seasonal mean counts. They have been accepted as fairly realistic ones since the variability introduced by the observers' inability to count correctly during heavy fish passage is known to be substantial although as yet not measured.

TABLE 1. Variation in estimated escapements of sockeye salmon at Igiugig, 1964–66.

Year	No. of counting days (n)	Mean count in 10 min	Variance of mean	SD[a]	C.V.	N[b]	95% confidence limits of N	
							Upper	Lower
1964	36	184.52	130.23	11.412	.303	956,574	1,053,201	859,947
1965	36	4640.83	12,104.32	110.02	.116	24,058,038	24,989,448	23,126,627
1966	29	890.03	1,785.16	422.51	.232	3,716,678	4,004,864	3,428,492
Avg	34	890.03			.217			

[a] Standard deviation.

[b] The final estimates differ slightly from those published by Alaska Department of Fish and Game since the very early and very late parts of the run were not considered here. This is so because of the irregularity of the counting schedule.

The distribution of the sample counts made during the season is positively skewed. However, the mean $\bar{x}$ of the counts can be approximated by a normal distribution. Consequently

$$\frac{1}{\hat{N}^2} \hat{\mathrm{Var}}\ \hat{N} = \frac{s_{\bar{x}}^2}{\bar{x}^2} = \frac{s_x^2}{n\bar{x}^2} = \frac{1}{n}\ (\mathrm{C.V.})^2 \qquad (4)$$

where C.V. is the coefficient of variation of the 10-min systematic sample counts, and n the total number of systematic samples.

If the standard deviation of the sample counts, s_x, is proportional to the mean, the coefficient of variation will be constant from year to year and any change in the value of equation 4 will depend on the number of counts, n, made each day during the season. This is not so for the three years examined (Table 1). However, since the escapements ranged from about 1 million to about 25 million spawners, Table 1 covers the entire range one can expect in the coefficient of variation.

This was smallest in 1965 with the largest escapement. This reflects a tendency to greater relative stability in the migration rate of heavier runs. However, the value would increase if there were a measure of the larger counting error involved in assessing large daily escapements. Furthermore, small changes do not alter drastically the value of expression 4, which is largely determined by the number of daily samples. Accordingly, if the number of sample counts per season remains relatively constant, the magnitude of the variance component contributed by estimation of the escapement size every year can be approximated by using an average number of sample counts and an average C.V. From the data in Table 1 an average coefficient of variation of .217 was determined and the season set to 34 days. Substituting these values in equation 5 yielded

$$\frac{1}{\hat{N}^2} \mathrm{Var}\ \hat{N} = .00139 \qquad (5).$$

ESTIMATION OF SEX RATIO

The normal procedure in sampling to determine the sex ratio in the escapement is to make a beach seine haul near the counting site for about 200 salmon on days when at least a few thousand fish are ascending. A daily sex ratio is determined from the entire seine sample, and it is multiplied by the daily escapement so as to determine the number of females ascending daily. Several days may be combined into one period when fish passage is light. From the sum of all daily (or period) estimates of the number of females in the escapement, the number of females and the sex ratio, P, in the entire run may be obtained.

For each year and all years combined, this parameter and its variance were estimated by

$$\hat{P} = \frac{1}{\hat{N}} \Sigma \frac{\hat{N}_i a_i}{n_i} = \frac{1}{\hat{N}} \Sigma \hat{N}_i P_i \text{ and } \hat{\mathrm{Var}}\, \hat{P} = \frac{1}{\hat{N}^2} \Sigma \hat{N}_i^2 \frac{P_i(1-P_i)}{n_i} \qquad (6)$$

where N = estimated total escapement; $\hat{N}_i$ = estimated escapement for period i; n_i = number of fish in the sample for period i; a_i = number of females in the sample for period i.

The approximate expression for the variance is permissible here since the sample size, n_i, forms an insignificant part of the daily escapement, N_i.

Over the years 1955 to 1966, the yearly sex ratio was determined from 17 to 27 seine samples. In all the years except two, females outnumbered males in the escapement, but never so greatly that a large number of unfertilized eggs could have resulted from the spawning (Mathisen, 1962).

An analysis of variance with a single classification between years was performed on the data for all years. An average variance of the sex ratio in individual years was used, although this quantity varied greatly from year to year (Table 2). The F-ratio was highly significant (F = 53.4 with 11 and 235 df).

In the estimation procedure, which utilizes an average sex ratio, a bias is introduced which will vary from year to year. The yearly ratios ranged from .42 to .67, although deviations from the common mean in general were much smaller (Table 2).

TABLE 2. Variation in sex ratio in the sockeye salmon escapement to the Kvichak River system, 1955–66.

Year	No. of samples (n)	Weighted sex ratio	Weighted variance of sex ratio $\times 10^3$	Deviation from the mean
1955	17	.5573	.198	+.0202
1956	26	.5151	.063	−.0220
1957	28	.5335	.075	−.0036
1958	13	.5044	.121	−.0327
1959	18	.5630	.163	+.0259
1960	22	.5655	.058	+.0284
1961	25	.6658	.076	+.1287
1962	19	.5117	.171	−.0254
1963	15	.4791	.203	−.0580
1964	22	.4173	.097	−.1198
1965	27	.5709	.104	+.0338
1966	15	.5618	.142	+.0247
Mean of all years	20.6	.5371	.123	

The variance component due to estimation of the sex ratio, $\frac{1}{\hat{P}^2}$ Vâr $\hat{P}$, was computed by using the average variance and sample size for all years combined. It was assumed that the sex ratio ranged from .40 to .60. The variance component was as follows:

	P	Vâr P	$\frac{1}{P^2}$ Vâr P
Individual years	.40–.60	$.123 \cdot 10^{-3}$	$(.769-.342)10^{-3}$

ESTIMATION OF AVERAGE LENGTH OF FEMALES

The length-frequency distribution of females in a season's escapement was determined from the length distribution of females captured in daily seine samples weighted according to daily escapement totals. Fortran programs prepared for this purpose by Gales (1963), DiCostanzo (1965), and McKenzie (1967) were used (Fig. 1 and Table 3). The four principal year-classes, 4_2, 5_3, 5_2, and 6_3, were divided into two groups, 2-ocean females and 3-ocean females. These two groups differed significantly in average length by more than 69 mm. Furthermore, the mean length of 2-ocean fish differed significantly between years, whereas that of 3-ocean females did not. The average difference in length

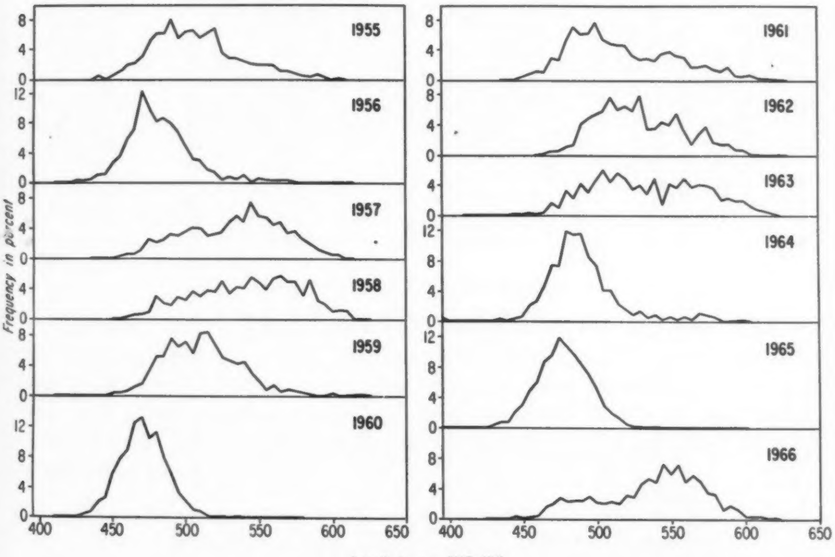

FIG. 1. Length frequency distributions of female sockeye escapements to the Kvichak River system, 1955–66. Length measured from the middle of the eye to the fork of the tail.

TABLE 3. Variation in mean lengths (mm) of age-groups of females in sockeye salmon escapements to the Kvichak River system, 1957–66.

	Age-group									
	4_2	5_3	2-ocean[a]			5_2	6_3	3-ocean[a]		
Year	$\bar{x}$	x	n	x	s^2	$\bar{x}$	$\bar{x}$	n	$\bar{x}$	s^2
1957	537.5	502.7	285	503.2	700.85	550.6	559.9	443	552.0	584.32
1958	493.2	519.7	128	516.8	812.54	559.5	569.0	158	567.7	774.39
1959	504.8	512.4	447	510.5	616.92	557.0	559.6	36	558.9	1030.14
1960	471.1	488.0	629	471.4	297.40	535.0	535.0	3	535.0	—[b]
1961	503.7	503.6	231	503.6	692.72	563.1	565.0	165	563.2	785.07
1962	515.0	511.2	211	511.3	521.43	566.2	561.4	86	562.3	672.75
1963	501.8	531.5	159	513.7	798.13	570.6	571.9	95	571.7	597.23
1964	486.1	499.7	1196	487.1	386.46	564.6	577.5	50	567.2	469.75
1965	482.5	477.3	2003	477.2	359.31	542.1	519.0	12	540.4	1302.08
1966	493.9	504.5	601	503.8	843.59	568.5	555.4	973	556.0	749.80
All years combined	493.6	505.1	5890	488.7	689.34	557.7	557.4	2021	557.7	734.84

[a] Includes additional measurements of fish with unknown freshwater age.
[b] Not determined because of few observations.

between 4_2 and 5_3 females amounted to about 11 mm and the average difference in length between 5_2 and 6_3 females was less than 1 mm.

Therefore, the principal factor that determines the average length of the females is the ratio of 2- and 3-ocean females. For the years 1955–66 the range of the deviation of the yearly means for both ocean age groups from the overall mean is from −7.9 to +6.1% (Table 4). These differences become important only to the extent to which they alter determination of average fecundity.

TABLE 4. Variation in mean lengths of females in escapements to the Kvichak River system, 1955–66.

Year	Mean length (*mm*)	Deviation of mean *mm*	Deviation of mean %
1955	507.9	-3.7	-.72
1956	484.2	-27.4	-5.36
1957	533.8	+22.2	+4.34
1958	542.6	+31.0	+6.06
1959	511.4	-.2	-.04
1960	471.3	-40.3	-7.88
1961	517.6	+6.0	+1.17
1962	530.3	+18.7	+3.66
1963	534.1	+22.5	+4.40
1964	491.6	-20.0	-3.91
1965	478.0	-33.6	-6.57
1966	536.0	+24.4	+4.77
Mean 1955–66	511.6		

ESTIMATION OF FECUNDITY

Fecundity samples were collected in the years 1964, 1965, and 1966 from different spawning streams or beaches of Iliamna Lake by personnel of the Fisheries Research Institute. Maturing females were collected with a beach seine, and a few samples were taken from the catch of the resident fishery, which utilized $5\frac{3}{8}$-inch gillnets. The numbers of samples collected from the various sites were:

Year	Cabin Bay	Moose Bay	Finn Bay	Pedro Bay	Knutson Bay	Iliamna River	Copper River	Newhalen River	Totals
1964	42	20	68	61					191
1965		42			42	40	38	62	224
1966		50			45	50	50	48	243

Length was measured from mideye either to fork of tail or to hypural plate, and all measurements by the latter method were converted to tailfork measurements (Duncan, MS, 1956).

The unbroken ovaries were submerged in boiling water for 5–10 min until all eggs hardened and loosened from the skeins. Eggs were removed from each ovary by hand, preserved in 4% formaldehyde in plastic bags, and counted 2 or 3 months later. Initially, an egg counter of the type developed and described by Davis and Paulik (1965) was used. Frequent adjustments of the diameter of the counting tube were necessary because eggs from 2-ocean females differed in size from those of 3-ocean females; therefore, half of the samples taken in 1964 and all samples taken in 1966 were counted manually.

Normally the relationship between fecundity and length is assumed to be a linear function on the log transformed variables (Scott, 1962). In this instance a direct linear relationship was used since the data consisted of two clusters of points around the mean lengths of 2- and 3-ocean females and with all the lengths in the range 450–600 mm. Scatter diagrams for the data for each of the 3 years confirmed that this was an acceptable approximation.

The regression lines were tested for common intercept, H_A, on the assumption of a common slope (Table 5) by an analysis of covariance (Dixon, 1965, BMDO1R). This hypothesis was rejected. An alternate hypothesis, H_B, that the regression lines have a common slope was likewise rejected.

TABLE 5. Analysis of covariance of fecundity vs. length, 1964–66.

Year	No. of samples	Hypothesis H_B, of a common slope		Hypothesis H_A, of a common intercept	
		F	df	F	df
1964–66	3	83.94[a]	2, 652	16.81[a]	2, 654
1964	4	1.11	3, 183	.16	3, 186
1965	5	1.78	4, 214	23.79[a]	4, 218
1966	5	5.54[a]	4, 233	15.22[a]	4, 237

[a] Denotes 1% points for the F distribution.

The situation is similar to that encountered with the sex ratio and average length of females. An average regression line will give a biased estimate of the fecundity corresponding to an average length of the females. But the variance about the single regression line is only slightly larger, $s^2_{y \cdot x} = .285 \cdot 10^6$, than the average variance about the individual regression lines, $s^2_{y \cdot x} = .264 \cdot 10^6$.

Since the regression lines for the years 1964, 1965, and 1966 were determined from samples different from those used for determination of average length of the females, the variance of $\hat{F} = a + b\,(x - \bar{x})$ was approximated by the delta method (Lindley, 1965):

$$V\hat{a}r\ \hat{F} = \text{Var}\ a + (x - \bar{x})^2\ \text{Var}\ b + b^2\ \text{Var}\ x \qquad (7).$$

By substituting in equation 7 the appropriate values derived elsewhere an estimate of the variance of $\hat{F}$ for each of the 3 years discussed above was obtained (Table 6). The three variance estimates were of the same magnitude.

Table 6. Variation in length and fecundity and variance estimates for 1964, 1965, and 1966.

Year	Mean length (*mm*)	Variance of means	Regression lines	Sample size	$s^2_{y\cdot x}$	$\Sigma(x-\bar{x})^2$	$\hat{\text{Var}}\ \hat{F}$	$\frac{1}{\hat{F}^2}\cdot\hat{\text{Var}}\ \hat{F}$
1964	491.6	.793	$F = 4088+12.06(x-511.6)$	191	$.186\cdot10^6$	$.284\cdot10^6$	1351.2	$.913\cdot10^{-4}$
1965	478.0	.410	$F = 3563+12.80(x-487.6)$	224	$.259\cdot10^6$	$.100\cdot10^6$	1461.9	$.123\cdot10^{-3}$
1966	536.0	.892	$F = 4164+9.55(x-542.1)$	243	$.348\cdot10^6$	$.312\cdot10^6$	1553.4	$.921\cdot10^{-4}$
1964–66			$F = 3937+10.89(x-514.7)$	658	$.285\cdot10^6$	$.104\cdot10^6$		

The variance around the regression lines can be reduced by increasing the sample size. But it seems more fruitful to examine sources of the great variability in the regression of fecundity on length as a preliminary for a future, more precise definition of the functional relationship.

The established difference in slope and intercept of the regression lines between years points to definite, although as yet largely unidentified, factors that contribute to the large variation around the regression lines. However, if one assumes that each race of sockeye salmon in the escapement possesses a specific fecundity–length relation, then the geographic distribution of the sampling effort is a source of variability between years.

A single yearly regression line could not be fitted to samples taken in each of the 3 years (Table 5), but a single regression line could be fitted to all samples in all years for one specific locality except for samples taken from Iliamna River. Obviously, then, the fecundity estimate of a salmon escapement should be based on samples taken throughout the season in the trunk stream, where all races are mixed according to their abundance (Smith, 1964).

Furthermore, fecundity may be best described by a curvilinear multiple regression curve with egg size as another factor. The variability in egg size for spawners in four types of spawning areas was examined in 1965, 1966, and 1967 by personnel of the Fisheries Research Institute. Approximately 200 eggs were extruded from each female captured with a beach seine when they were actively spawning. The length of each fish was measured, and the eggs were hardened in water for at least 2 hr. A 12-inch egg trough was filled, and eggs required to fill the trough were counted manually. Three replicate determinations were made, and the mean egg size was calculated. Samples were then grouped according to spawning ground type. There are four principal types of spawning grounds in the Kvichak River system: rivers and streams, springfed ponds, mainland beaches, and island beaches.

Samples from all 3 years from each type of spawning ground were combined and a regression line was computed for each type and for all samples combined (Table 7).

TABLE 7. Regression lines of mean egg sizes on lengths for spawning females collected from four types of spawning grounds in Iliamna Lake, 1965, 1966, and 1967.

Type of spawning ground	No. of observations	Regression line
Streams and creeks	535	$Y = 81.14-0.502X$
Spring-fed ponds	141	$Y = 80.82-0.492X$
Mainland beaches	368	$Y = 80.97-0.491X$
Island beaches	732	$Y = 76.90-0.480X$
H_A: F = 396.7		df: 3, 1771
H_B: F = .19		df: 3, 1768

The hypothesis that the regression lines have a common slope was sustained but the hypothesis that a single regression line can be fitted to all data was rejected. Figure 2, in which the four regression lines are depicted, demonstrates clearly the differences in egg size between females taken on island beaches and females taken from the three other types of spawning grounds and the common slopes of their regression lines. (The figure gives the inverse of egg size measured as the number of eggs required to fill a 12-inch egg trough.)

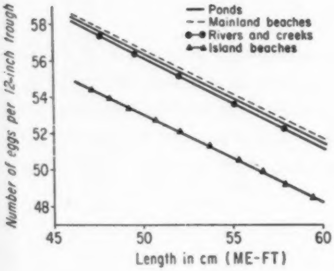

FIG. 2. Regression lines of egg sizes on lengths of females from four types of spawning grounds, 1965, 1966, and 1967. Length measured from the middle of the eye to the fork of the tail.

Since the spawning areas were occupied by independent groups of spawners, it appears that egg size is a manifestation of racial character. But it does not necessarily follow that the island beach spawners, which produced the largest eggs, were lowest in fecundity among the races. The effect of egg size on fecundity can be isolated only by multiple regression techniques, which the present material does not allow.

DISCUSSION

The variance of the potential egg deposition represented by a year's escapement was approximated by equation 2. The components of the variance for an average escapement (74% 2-ocean and 26% 3-ocean fish) to the Kvichak District were computed (equation 5 and Table 6). In summary, the estimated variance of PE is between

$$V\hat{a}r\ PE = PE^2\ [.135 \cdot 10^{-2} + .342 \cdot 10^{-3} + .913 \cdot 10^{-4}]$$

$$V\hat{a}r\ PE = PE^2\ [.135 \cdot 10^{-2} + .769 \cdot 10^{-3} + 1.23 \cdot 10^{-4}]$$

where the limits established for the range of sex ratios in 1955–66 and the fecundity estimates for 1964–66 are used.

The largest variance component is due to estimation of the escapement, which is an unbiased estimate with the present counting scheme. Greater counting effort in the future will reduce this variance component, but it seems desirable to replace the present systematic counting scheme with a design stratified according to the daily escapement size.

Since the escapement curve as a function of time is domeshaped, one may tentatively suggest the establishment of three strata: the first covering the first 20% of the run, the second including the next 60% of the run, and the third representing the remainder. Such a division can be made because of the fairly regular shape of the escapement curve at the counting site and the fact that the time schedule can be adjusted by taking the commercial catches about 1 week earlier (Royce, 1965). The problem is, then, to minimize

$$K = s^2_{\bar{\bar{x}}} + \lambda(n_1 + n_2 + n_3 - n)$$

where $s^2_{\bar{\bar{x}}}$ is the estimated weighted variance of the mean count for the three strata and the expended counting effort is n_1, n_2, and n_3 periods out of a seasonal total of n counting periods. The finite population correction has been omitted here. The Langrage multiplier, λ, is found by partial differentiation with respect to the variable parameters and equating these to zero. This yields, according to Cochran (1963),

$$n_i = \frac{W_i s_i}{\Sigma(W_i s_i)} n.$$

The weights W_1 and $W_3 = .2$ and $W_2 = .6$ and s_i is the estimated standard deviation within stratum i. Other strategies for creating homogeneous strata can be established today from observations made during the past 13 years.

In general, the variance of the counts will be least during the peak of the run, when the passage rate of the ascending salmon is fairly uniform, provided that the observers can correctly count the fish passing. This condition is obviously not met when counting must be done in groups of 5, 10, or even larger units of fish. Simultaneous duplicate counts are needed in these instances, and this source of variance must be included before a final sampling scheme can be suggested in addition to the variability of counts within any hour.

The sex ratio and the length distribution of the females must be estimated each year because there are significant differences between the years.

The error from the use of an average proportion of females for all years is usually about ±5% but is as high as 19 and 29% for 2 years (Table 8). A doubling of the sampling effort would reduce the variance of the particular parameter in question. Any further reduction does not seem warranted when one considers the component that it will contribute to the variance of the potential egg deposition.

Similarly in regard to estimation of average length, since the ocean age composition of the female escapement may range from exclusively 2-ocean fish through different ratios of 2- and 3-ocean fish to only 3-ocean fish or nearly so, a common average length may be strongly biased in either positive or negative direction. But an increase in length measurements serves a useful purpose only if a close relationship can be defined between fecundity and length, whereby

TABLE 8. Percentage errors in estimating the number of females from an average proportion of females, 1955–66.

Year	Escapement in 1000's	Observed sex ratio	Estimated no. of females in 1000's: Observed	Estimated no. of females in 1000's: Computed	% error
1955	251	.5573	140	135	−3.57
1956	9,443	.5151	4,864	5,072	+4.28
1957	2,843	.5335	1,517	1,527	+.66
1958	535	.5044	270	287	+6.30
1959	680	.5630	383	365	+4.70
1960	14,630	.5655	8,273	7,858	−5.02
1961	3,706	.6658	2,467	1,990	−19.34
1962	2,581	.5117	1,321	1,386	−4.92
1963	339	.4791	162	182	+12.35
1964	957	.4173	399	514	+28.82
1965	24,326	.5709	13,888	13,065	−5.93
1966	3,775	.5618	2,121	2,028	−4.38

average fecundity can be estimated by a regression technique. Because of the variability among individual spawning grounds, a functional relationship can be established best from samples taken in the trunk stream throughout the duration of the run. Recently developed egg-cleaning machines and improved photoelectric egg counters should aid materially in reducing the labor involved in fecundity determination.

The sockeye salmon runs to the Kvichak River system exhibit a cyclic shift in abundance, in sex ratio, and in the ratios of 2- and 3-ocean fish. Therefore, it is highly conceivable that after intensive observations for 2 or 3 more cycles, a pattern will emerge and the average sex ratio and length of females can be defined for each year of the cycle, which will eliminate any need for yearly observations of length and sex ratio.

The magnitude of error accruing from the use of average values for the sex ratio, length, and fecundity is not constant from year to year, and of considerable magnitude in certain years (Table 9). The deviation in 1964 is caused

TABLE 9. Percentage errors in estimating the potential egg deposition from mean values of the sex ratio, length of females, and fecundity, 1964–66.

Year	Potential egg deposition: Yearly parameters	Potential egg deposition: Avg parameters	% error	95% confidence limits of yearly estimate
1964	$1.535 \cdot 10^9$	$2.005 \cdot 10^9$	+30.6	$(1.334\text{–}1.736) \cdot 10^9$
1965	$47.247 \cdot 10^9$	$50.433 \cdot 10^9$	+6.7	$(44.319\text{–}50.175) \cdot 10^9$
1966	$8.573 \cdot 10^9$	$7.782 \cdot 10^9$	−9.1	$(7.096\text{–}9.876) \cdot 10^9$

primarily by deviation in the sex ratio from the average sex ratio established for all years. The biased estimates of PE from average parameter values were outside the 95% confidence limits in 2 out of 3 years..

The potential egg deposition can be estimates with any desired degree of accuracy by increasing sample size in all steps of the estimation procedure. Relatively minor changes can be made either in the total expended effort or in the relationship between the various steps with the present crew of three men. Large improvements can be achieved only by adding personnel. The final value of such a course is not yet clear since the residual variance in spawner-recruit curves proceeds from all sources from the time of egg deposition to the return of mature spawners. These sources and the magnitudes of their contributions are still largely unknown. Therefore, the real gain in improvement of estimation of potential egg deposition cannot be determined at the present time.

ACKNOWLEDGMENTS

We are indebted to our colleagues Dr D. E. Rogers and Mr W. H. Lenarz for fruitful discussions of various aspects of the subject. Dr Rogers read the first draft of the manuscript and suggested the organization followed in the present paper.

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Age Determination from Scales of Chum Salmon (*Oncorhynchus keta*)

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LALANNE, JOHN J., AND GUNNAR SAFSTEN. 1969. *Age determination from scales of chum salmon (Oncorhynchus keta).* J. Fish. Res. Bd. Canada 26: 671–681.

The methodology of age determination from scales of chum salmon (*Oncorhynchus keta*) is reviewed. Scales from chum salmon caught in the North Pacific Ocean and streams of North America were studied. Most annuli are of two main types: a poorly formed circulus usually "cut over" by the first circulus of new growth, and what appears to be a normal circulus in the annual ring. The annulus of type 1 may be independent of the annual ring. Annuli may be at the anterior or posterior margins of the annual ring, or within it. Direct evidence that annuli are recognizable age indices was obtained from scales of marked fish.

An average of 98% of the age determinations by three scale readers agreed with the known age of the fish. The time of annulus formation or start of new growth extends from as early as March to the end of June and possibly to the end of July. The annual ring begins to form near the end of the season (as early as August) or when new growth occurs in the spring or summer. Sometimes an annual ring is not formed. Scales taken from various parts of the body had the same number of annuli.

Received June 11, 1968

INTRODUCTION

GOVERNMENT AGENCIES OF Canada, Japan, and the United States began research in 1955 for the International North Pacific Fisheries Commission (INPFC) to identify Asian and North American salmon on the high seas and to determine the distribution and extent of intermingling of the stocks. Among the data studied were patterns of scale growth that reflect various stages in the life history of the fish. Differences in scales can be used to identify stocks and can provide information on age and growth. Methods of collecting scales, counting and measuring scale characters, and the problems of age determination for chum salmon (*Oncorhynchus keta*) were reviewed in an earlier paper (LaLanne, 1963). The present report evaluates some of the basic assumptions required for valid age determination and directs attention to problem areas.

MATERIALS AND METHODS

Materials used in this study were scale samples taken from maturing and immature chum salmon in the North Pacific Ocean and from adult fish in several North American streams. Except where otherwise stated, scales were taken from a particular location on the body. The key scale is on either the right or left side, two rows above the lateral line on a diagonal row of scales that proceeds ventroposteriorly from the posterior insertion of the dorsal fin.

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Scales[1] were affixed to a gummed card and impressions made on a plastic card for microscopic examination (Clutter and Whitesel, 1956). A microprojection device of the type described by Mosher (1950) was used to examine enlarged images of the scale impressions. Ages were determined at magnifications of 100× and 42×. Photographs of the projected images were made on high-contrast film, and enlarged.

Age designations in this report follow the system of Koo (1962). For adult salmon the number of winters in fresh water after hatching is shown by an Arabic numeral followed by a dot; the number of winters at sea is shown by an Arabic numeral preceded by a dot. Fry of chum salmon do not spend a winter in fresh water; consequently, they are of zero freshwater age. The zero is usually omitted from the age designation. We chose January 1 as the reference date to designate age. Thus, from the time of hatching until December 31 of its first winter at sea, a chum salmon is in age-group .0; from January 1 until December 31 of the following year the fish is in age-group .1 and so on. The annulus is usually not formed until after January 1 — therefore, a virtual annulus is accredited to the scale if the annulus of the current year is absent.

DETERMINATION OF AGE FROM SCALES

The soundness of age determination of salmon from scales depends on the validity of the following basic assumptions: (1) Recognizable year marks are laid down on the scale each year. (2) Year marks are formed at about the same time for all members, or the time of formation is known for the stock. (3) All scales on a fish have the same number of year marks. (4) Regenerated[2] and normal scales can be distinguished. (5) The degree of resorption[3] can be determined by visual inspection of the scale.

Description of the Scale

The outer surface of the scales of chum salmon is sculptured with a series of circular and semi-circular ridges, or circuli, mainly on the anterior part of the scale; this sculptured portion is oriented anteriorly on the fish and is imbedded in a dermal pocket. Changes in the rate of scale growth are reflected in the width and spacing of the circuli. Thick and widely spaced circuli reflect rapid scale growth and narrow, closely spaced circuli reflect slow scale growth. It is commonly assumed that in the temperate zone scales grow rapidly in the spring and summer and slowly or not at all in the fall and winter, and that consequently a band of widely spaced circuli followed by a band of closely spaced circuli constitutes an annual field of growth.

In most studies of scales of Pacific salmon, the band of crowded circuli was considered the year mark and was commonly called the annulus. Additional terms, such as winter check, annual band, winter ring, resting zone, were also used for the band of crowded circuli. Apparently until recently there was no term to define the circulus, or definite point or boundary, between the annual fields of growth on scales of salmon. In studies of age and growth of many other fishes the term "annulus" has been used for the boundary.

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[1] The term "scale" in this report refers either to a plastic impression or to the scale itself. Usually the distinction between the two is obvious or immaterial. Where necessary, one or the other is specified.

[2] Regeneration is the process by which new scales are formed to replace those lost.

[3] Resorption mainly occurs near spawning time and involves the gradual disintegration of the scales.

"Annulus" has been used also for the boundary between the annual zones in some studies of Pacific salmon scales. Ricker (1962) wrote for scales of sockeye salmon (*O. nerka*): "The growth years are separated by the scale annuli, the point of division being the outer margin of the closely spaced circuli or 'winter ring'." Bilton and Ricker (1965) defined the annulus of scales of pink salmon (*O. gorbuscha*) and chum salmon as the outer margin of the winter check. Pearson (1966), writing on pink salmon, said: "The annulus is the last narrow circulus of the winter ring." On scales of chum and pink salmon, Bilton and Ludwig (1966) called a band of closely spaced circuli the annual ring and defined the annulus as "the last narrowly spaced circulus of the annual ring preceding the first, more widely spaced, circulus referred to here as the start of 'new' growth."

In the present paper the circulus between the annual fields of growth is called the annulus or year mark. A band of relatively closely spaced circuli when in conjunction with an annulus is called an annual ring. The thick and widely spaced circuli are termed summer circuli or summer growth, and the part of the scale formed immediately after the annulus is termed new growth. The growth beyond the last annulus is called marginal growth.

Most annuli on scales of chum salmon are of two main types and the annuli are not always at the outer edge of the annual ring. These conclusions are based on an examination of the circuli that compose the annulus and annual ring and of scale samples taken during the period of annual ring formation.

A scale from a chum salmon caught in autumn, with all or part of the annual ring present at the margin is shown in Fig. 1. The fish was one of 159 (caught on September 16, 1962), of which 42% had scales with a band of closely spaced circuli at the margin. The ring appeared on scales of fish of all age-groups (.0–.4) in the sample. One would expect to find the annual ring at the margin of the scales of chum salmon caught in the winter and spring before new growth started at the margin. An example from a chum salmon caught in the winter on February 20, 1963, is shown in Fig. 2. The ring at the margin was probably formed in the fall or winter. It is possible that these marginal marks are supplementary checks caused by reduced scale growth outside the time of formation of the annual ring (Fig. 4). The position of the marks relative to the focus and the penultimate annulus suggest, however that they are annual rings.

Some chum salmon caught in the winter did not have an annual ring at the margin of their scales. A scale (Fig. 3) from a chum salmon caught on February 8, 1963, shows no evidence of a ring at the edge. Marginal growth of this scale (13 circuli) was too large to be growth of the current year; it was evidently from the previous year. Scales with three annuli and from chum salmon caught in April 1962 had only one to five marginal circuli (Table 1, Group B, age-group .3). It is doubtful that a ring is formed at the margin later in the season on scales of the type shown in Fig. 3. Chum salmon with scales similar to those in Fig. 3 were captured as late in the season as May

TABLE 1. Number of marginal circuli of two groups of chum salmon (A and B) sampled in Gulf of Alaska during spring.

Date and location of sampling	Age-group	No. of circuli																						No. of fish
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
									A															
March 30, 1962 at 47°N 155°W,	.2	–	–	–	–	–	–	–	–	–	–	1	4	–	–	2	1	2	2	1	–	–	1	14
and	.3	–	–	–	–	–	–	2	1	3	5	2	2	–	–	–	–	–	–	–	–	–	–	15
April 1, 1962 at 46°N 155°W	.4	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1
									B															
April 6, 1962 at 46°54′N 142°15′W,																								
and	.2	–	–	2	–	1	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5
April 9, 1962 at 47°43′N 133°01′W	.3	1	2	4	3	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11

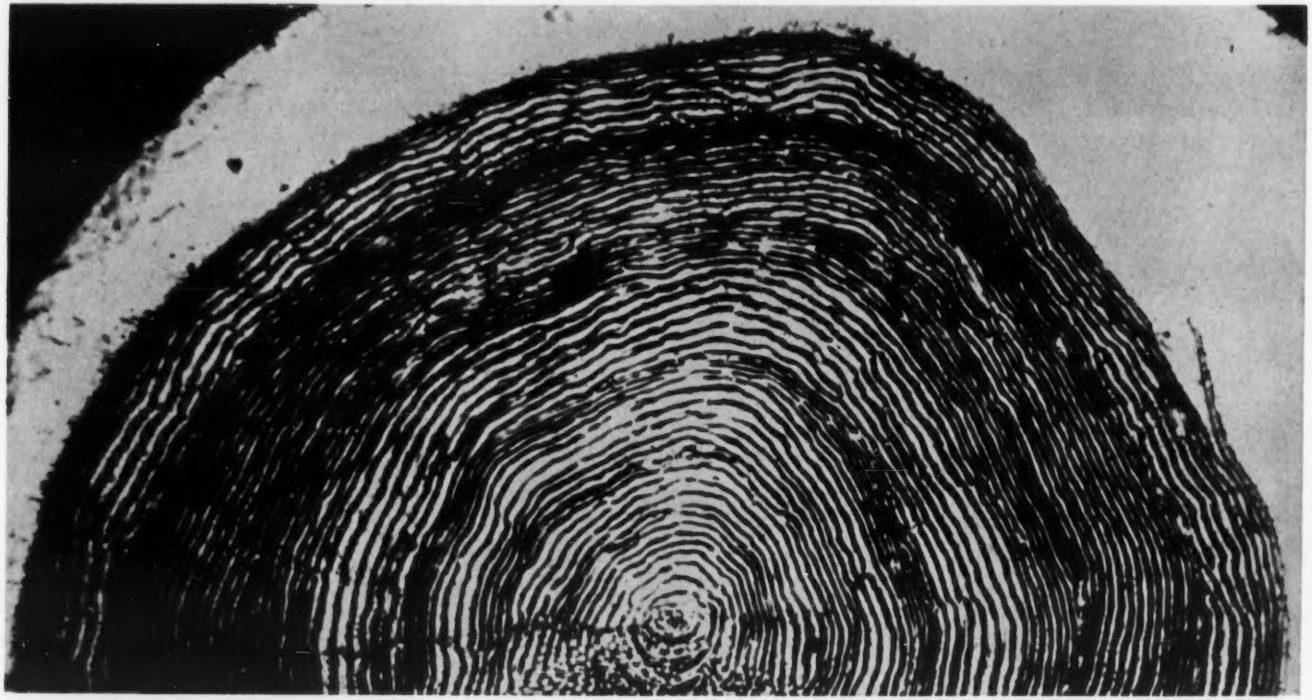

FIG. 1. Scale from a chum salmon in age-group .3 caught on September 16, 1962, at 51°45′N and 162°59′W. Band of closely spaced circuli at margin of scale is assumed to represent all or part of an annual ring formed in autumn.

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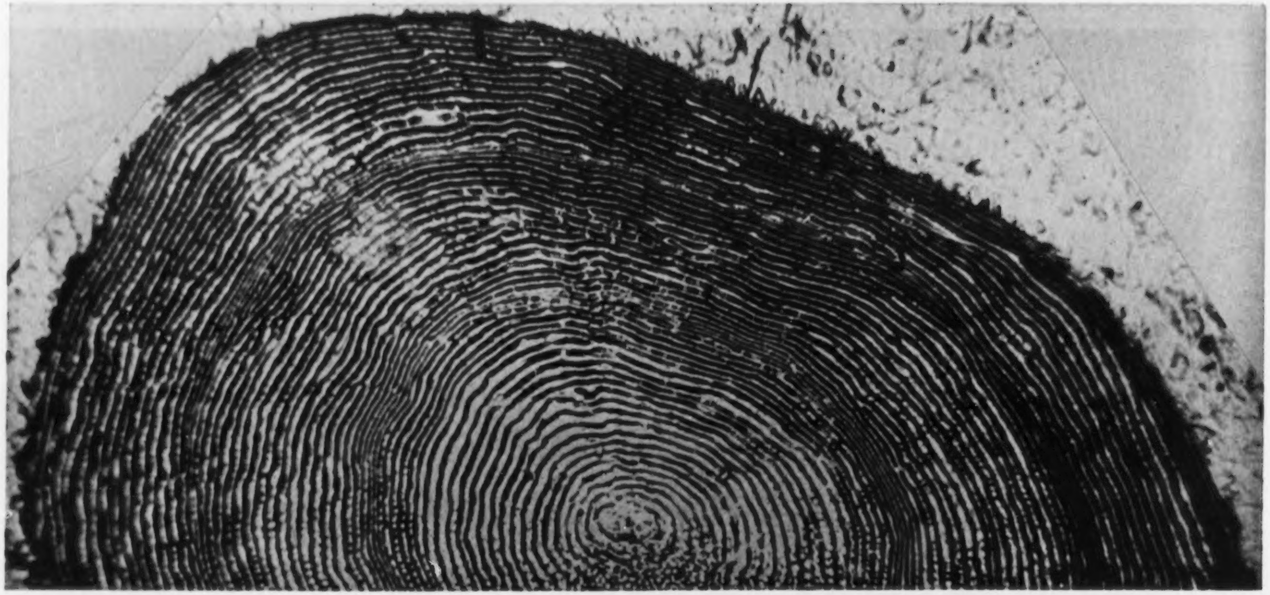

FIG. 2. Scale from a chum salmon in age-group. 3 caught on February 20, 1963, at 46°58′N and 179°55′E. Note all or part of the annual ring at margin of scale in winter.

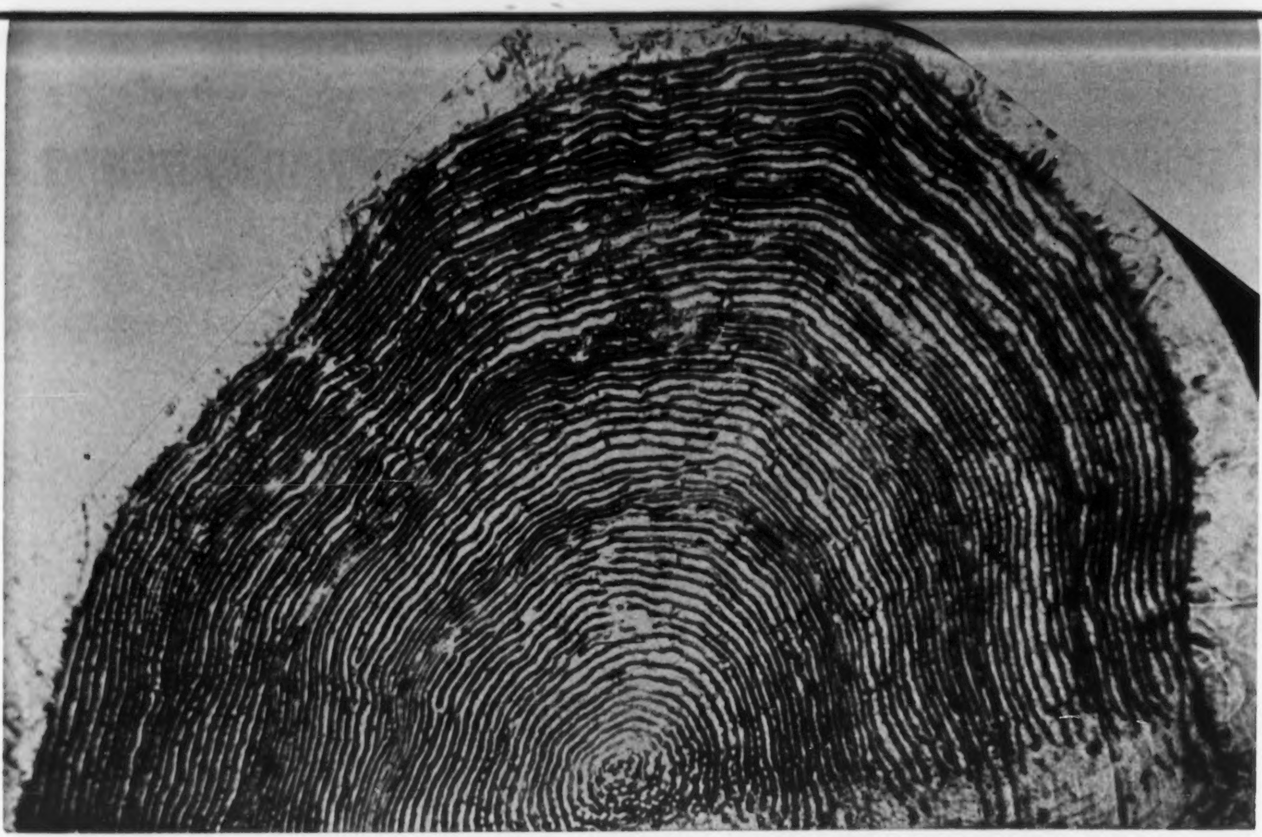

FIG. 3. Scale from a chum salmon in age-group .4 caught on February 8, 1963, at 53°28′N and 175°14′E. Note lack of annual ring at margin of scale in winter.

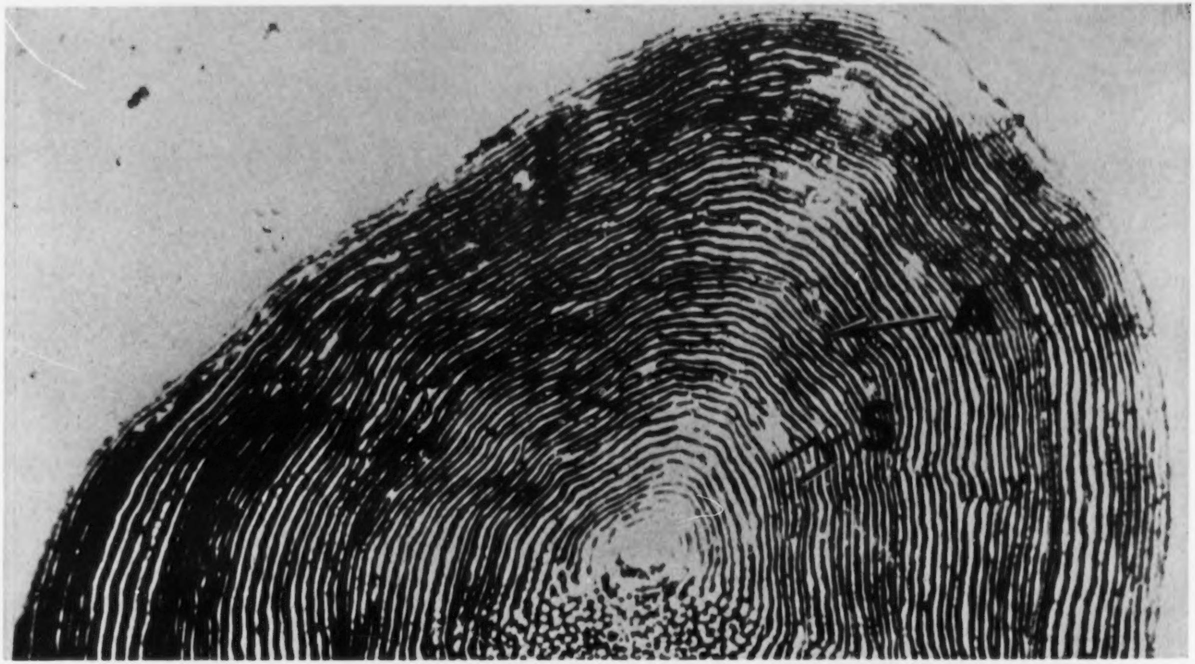

FIG. 4. Scale from a chum salmon showing a supplementary check (S) and a type 1 annulus (A) without annual ring.

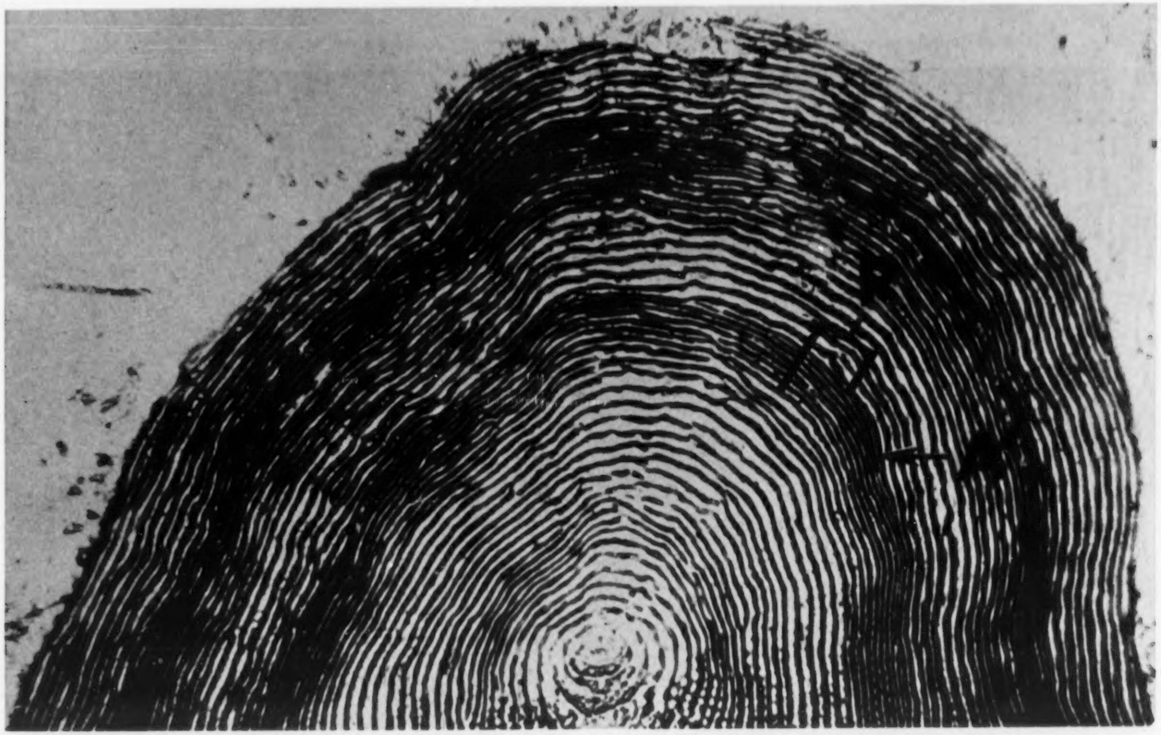

FIG. 5. Scale from a chum salmon showing a type 1 annulus (A) at the outer edge of a well-defined annual ring (R).

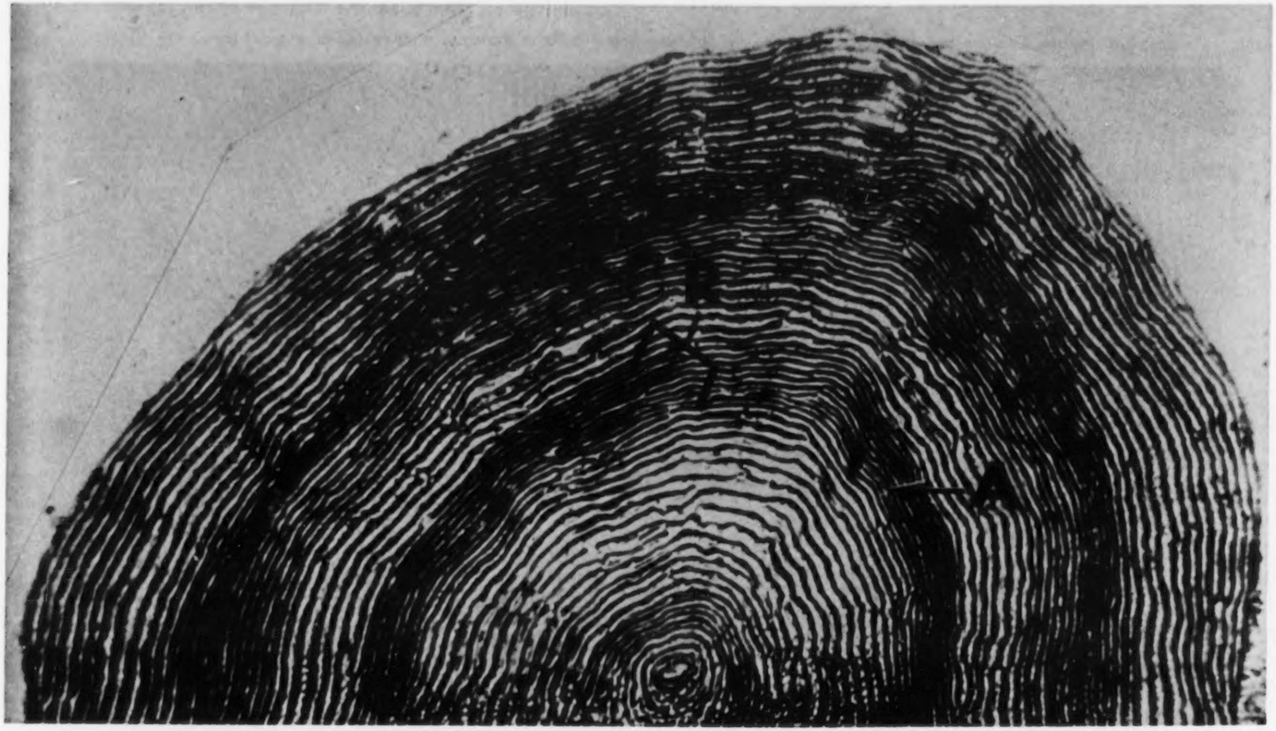

FIG. 6. Scale from a chum salmon showing annulus of type 1 (A) at the inner edge of the annual ring (R).

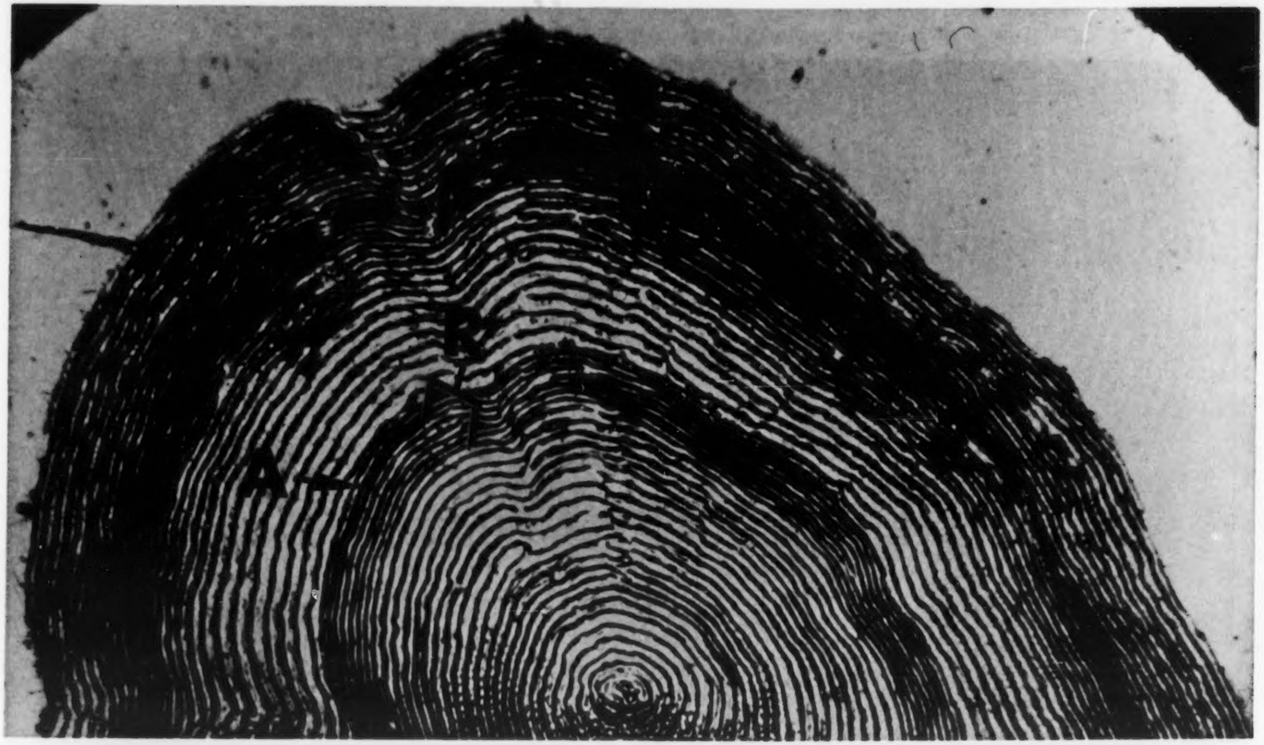

FIG. 7. Scale from a chum salmon showing annulus of type 2 (A) at outer edge of the annual ring (R).

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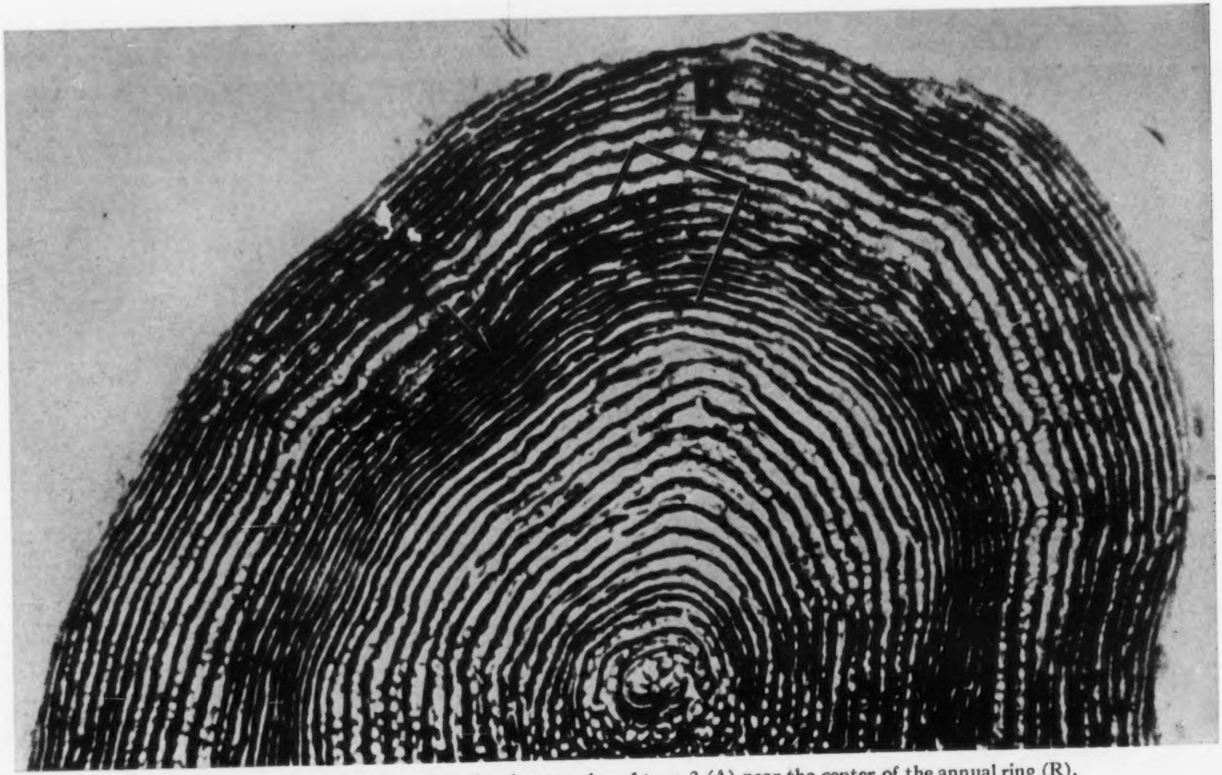

FIG. 8. Scale from a chum salmon showing annulus of type 2 (A) near the center of the annual ring (R).

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and June (Kobayashi, 1959). The fish were apparently in age group .3 but the marginal growth was unusually large for May and June (6-17 circuli). Kobayashi compared the scale characteristics and body lengths of these fish with those of chum salmon in age group .3 with small marginal growth and those in age group .4. The characteristics of those with large marginal growth and apparently in age group .3 were similar to those in age group .4. He concluded that the marginal growth was of the previous year; an annual ring had not formed.

If an annual ring is not formed prior to new scale growth and new scale growth resumes at a rapid rate, an annulus should result similar to that shown in Fig. 4. The annual ring is not apparent, only the annulus is present. This annulus is the basis for the definition of one of the two types of annuli that are most common on the scales of chum salmon. The annulus of type 1 is identified by several features. Usually one or two circuli at the boundary are poorly formed, faint, and fragmented. The fragments are often "cut over" by the first circulus of new growth (Fig. 4). If more than one faint and poorly formed circulus is at the boundary, the one farthest from the focus is the annulus. The annulus of type 1 is usually at the outer edge of the annual ring (Fig. 5). This presumably results when an annual ring is formed at the end of the season and new growth resumes at a rapid rate in the spring. The annulus of type 1 may be at the inner edge of the annual ring (Fig. 6). This occurs when a ring is not formed at the end of the season as in Fig. 3 and new scale growth proceeds at a slow rate.

Sometimes the growth of the scale is such that fragmented circuli and a "cut over" pattern are not formed at the boundary between the annual zones of growth .The annulus is a well-formed circulus of normal appearance within the annual ring. Two criteria are usually sufficient to locate the annulus of type 2:

(1) If the width of the circuli and interspaces in the ring are similar (Fig. 7), the annulus is the last closely spaced circulus of the annual ring preceeding the first circulus of new growth.

(2) The width of the circuli and interspaces of the annual ring may reflect a change in the rate of scale growth within the ring. In Fig. 8 approximately the inner half of the ring is assumed to reflect a gradually decreasing rate of scale growth at the end of the season (successive circuli thinner and more closely spaced); the outer half reflects a gradually increasing rate of scale growth at the beginning of the next season (successive circuli thicker and more widely spaced). The annulus is the narrowest circulus bracketed by the narrowest interspaces in the annual ring. If there is more than one "narrowest circulus", the one farthest from the focus is chosen.

The variability in the position of the annulus relative to the annual ring could be important in studies that relate scale growth to the growth of the fish. These studies usually require measurements of the yearly increments of scale growth. The outer edge of the last (outer) circulus of the annual ring is sometimes used as the boundary of the yearly increments of scale growth.

If this criterion is used for annual rings as shown in Fig. 6 and 8, more than one season's, growth would be included in the yearly increments. The annulus as defined here reduces this type of error.

Supplementary or accessory checks (Fig. 4) are similar to annuli and annual rings. No definite criteria can be given for the detection of checks as supplementary. They are usually recognized by their unusual position in the pattern of scale growth and often cannot be traced around the entire sculptured portion. The annulus and annual ring occur at regularly spaced intervals on the scale; they are roughly parallel to the margin and usually may be traced around the entire sculptured portion.

CONFIRMATION OF YEAR MARKS

Proof of the assumption that recognizable annuli appear on the scales of chum salmon can be obtained by examination of scales of fish of known age. LaLanne (1963) reported age determinations from scales of returning adults, marked as wild fry by removal of fins. Errors by two scale readers were 1 in 88 and 3 in 81, an average agreement of 97%. A later review of the readings showed that in all four of the incorrect determinations, fish in age-group .3 had been classified as age-group .4. One of the four errors was due to the inclusion of a supplementary check; the remaining three errors resulted from overestimates of resorption. The problem of errors in age determination due to scale resorption is discussed in a later section entitled "Effect of Regeneration and Resorption."

Bilton and Ricker (1965) examined scales of 14 chum salmon of known age (returning adults, marked as fry by removal of fins). All age determinations were the same as the known ages of the fish (100% agreement). Twelve of the 14 scales had a supplementary check near the focus. The basis for excluding the checks was that they generally were less distinct than annuli and were relatively near the focus. These studies support the assumption that scales of chum salmon do have recognizable annuli.

TIME OF ANNULUS FORMATION AND START OF NEW GROWTH

Reliable estimates of age and growth from scales require fairly accurate knowledge of the time of annulus formation and the start of new growth. The annulus or boundary between the annual fields of growth is not apparent until new scale growth has begun. To get the range in time of annulus formation, therefore, knowledge is required of the period when new scale growth starts on any of the fish. The data from scales of 46 chum salmon (Table 1) provide information on the beginning of new growth and also show contrasts in the scale growth among fish in two samples taken at nearly the same time and place (possibly two stocks involved).

The two samples listed as group A in Table 1 were taken March 30 and April 1, 1962, at 47° and 46°N lat at 155°W long. All of the scales had a relatively large number of circuli beyond the last annulus (range 7–22 circuli).

This marginal growth was considered too large to have been accomplished by April 1 of the current season. It was judged to be growth of the previous season, in other words, new growth of the current season had not occurred on the scales of fish in group A. The two samples listed as group B were taken a few days later on April 6 and 9 at 46°54′N lat, 142°15′W long, and 47°43′N lat, 133°01′W long. The growth beyond the last annulus ranged from one to six circuli. This marginal growth was too small to be growth of the previous season; it was judged to be new growth. Very likely most of the chum salmon in group B began new scale growth before early April, possibly early in March. Scales of the fish in the younger age-groups had the greatest marginal growth; they apparently resumed new growth earlier, grew faster, or both.

Additional information on the start of new scale growth was presented by Kobayashi (1959). Data in table V of his report showed that most of the chum salmon in age-group .3 in samples taken during 1956 in the North Pacific Ocean (exact location not given) had begun new scale growth by May 31. From June 21-30, 1.6% of the fish in age-group .4 had no new scale growth, but by July 1 all had at least one new circulus. Bilton and Ludwig (1966) reported no new growth at the periphery of scales of chum salmon taken in the Gulf of Alaska in January 1964 and 1965. Scales of fish caught during April 1964 had new growth (range 2–10 circuli), which had probably started in February or March. Gilbert (1922) mentioned that a few chum salmon in the Yukon River had no new scale growth as late as July 31. Thus, the time of annulus formation or start of new growth extends from as early as March to the end of June and possibly to the end of July.

Effect of Variable Scale Growth

The long interval before new growth leads to a major problem in determination of age. At the middle and late periods of the interval, scales that started new growth early in the season may have considerable marginal growth beyond the last annulus. Others that had not yet started new growth would have growth of the previous year beyond the last annulus. The marginal growth of the two types of scales may be similar in appearance, but an additional year (virtual annulus)should be added to the apparent age of fish with scales of the latter type. Information on the annual ring and rate of new growth can sometimes be used to distinguish marginal growth of the current and previous year.

In the previous section the annual ring was shown to form at the end of the season on scales of some chum salmon; the ring is present at the margin of the scales in the following spring before new growth appears. The ring at the margin in the spring indicates that the marginal growth is that of the previous year; an additional year (virtual annulus)should be added to the apparent age. If the marginal growth is suspected of being growth of the previous year and there is no annual ring at the edge, the decision whether to add a year is based on the number of marginal circuli expected at the time the fish caught.

Kobayashi (1959) furnished criteria on the amount of marginal growth expected before a year should be added to the age of chum salmon caught in May and June in the North Pacific Ocean. He recommended the addition of a virtual annulus to those apparently in age-group .3 that had six or more circuli beyond the third year mark. As noted before, however, the time new scale growth resumes can differ considerably among chum salmon caught on the high seas. The amount of marginal scale growth at a particular time of year can differ accordingly. For example, the fish in age-group .3 of group B of Table 1 (caught in April) had one to five marginal circuli. By May or June, additional growth would probably be added to the scale margin. If these fish (age-group .3 of group B) were sampled in May or June, many might have six or more marginal circuli. Application of Kobayashi's criterion in the age determinations would give incorrect classification to age-group .4. Knowledge of the characteristic scale growth and distribution of the many chum salmon populations on the high seas is needed to substantiate age determination based on the assumption that marginal growth of a certain magnitude is of the previous year.

An additional problem arises if Gilbert's observation of no new growth (for some chum slamon in the Yukon River) as late as July 31 is valid. The question of whether marginal growth was of the current or previous year then arises for fish caught inshore, especially those entering rivers early in the season. Figures 293 and 296 of Gilbert (1922) showed annual rings at the periphery of the scales of chum salmon caught on July 31; the scales were similar to those in our Fig. 1 and 2. Gilbert evidently assumed that new growth of the year was absent, and he included a virtual annulus at the scale margin in his age determinations. The new growth may have been absent because it had been resorbed. Gilbert was well informed on the problem of resorption, however, and it is doubtful that this was a factor (Gilbert, 1915). Another possibility is that considerable growth had occurred and that the annual ring at the edge of the scales was the result of retarded scale growth toward the end of the current growing season (Fig. 1). Gilbert evidently did not have evidence that some chum salmon may lack an annual ring at the edge of the scale before new growth, as shown in our Fig. 4 and 6. If new growth has not occurred for some inshore samples, the scale reader must also add a year to the age of fish with marginal growth of the previous year and no ring at the scale margin. To differentiate growth of current and previous years of this type for inshore samples could be very difficult.

Clearly, the time of annulus and annual ring formation can vary widely in chum salmon. Further knowledge of these factors is necessary to improve the accuracy of age determination of chum salmon from scales.

EFFECT OF LOCATION ON THE BODY

It is essential to know whether all scales on a chum salmon depict the same age. An attempt is usually made to sample scales from a particular location on the body, but regenerated or missing scales often make it necessary to sample from other locations.

Failure of all scales to give the same age may be traced to several reasons: (1) some scales may form later in life and therefore not have the same number of annuli; (2) regenerated scales of some fishes tend to resume normal appearance—regenerated scales of goldfish (*Carassius auratus*) could not be distinguished from normal scales after 180 days (Suzuki, 1952), regenerated scales of the mud loach (*Misgurnus anguillicaudatus*) resembled normal scales after 172 days (Kobayashi and Kawai, 1960), and those of Crucian carp (*Carassius carassius*) appeared normal after 3 weeks (Saito, 1955)—and although there is no such evidence for salmonids, regenerated scales of chum salmon might resume normal appearance without forming the normal number of year marks; and (3) when it is necessary to count the number of marginal circuli to determine age, variation of the count due to the body position of the scale could affect age determination.

We examined 610 scales from most of the body area of a chum salmon caught in the Kuskokwim River on July 2, 1958. The scales gave no evidence of resorption. The scales were randomly mixed with those from other chum salmon to eliminate bias; all readable scales had the same number of annuli. We did not determine the variation in the number of marginal circuli because of the possibility of undetected resorption. Scales from fish caught at sea would be more appropriate for determination of this variation.

EFFECT OF REGENERATION AND RESORPTION

The possibility that regenerated scales may return to normal appearance and yet lack the normal number of annuli has already been discussed. Blair (1942) described another possible source of variation in scale characteristics due to regeneration. Growth was retarded in scales adjacent to a large group of regenerated ones on an Atlantic salmon (*Salmo salar*); a band of closely spaced circuli was formed at the time of most rapid growth of the regenerating scales. Diversion of scale material to the area of regeneration presumably retarded growth. Scales taken farther from the regenerated area had normal circuli in the same part of the scale. This phenomenon could be an important cause of supplementary checks on scales. June and Roithmayr (1960) found that supplementary checks rarely were present on all the scales of an Atlantic menhaden (*Brevoortia tyrannus*), which fact indicates localized reduction of scale growth.

The effects of regeneration on growth of scales have not been studied for chum salmon. Such studies might well be incorporated into tagging and marking programs; removal of a small group of scales from the fish at tagging or marking and the subsequent recovery of the fish and the pertinent scales could further our knowledge.

Most of the scales taken from chum salmon caught in streams and estuaries show evidence of resorption. When resorbed scales are used for age determination, the scale reader has assumed that the portion of the original scale that remains is sufficient. Since no scientifically established method of measuring resorption is available, estimates are usually intuitive. Errors in age determination will occur if the amount of resorption is underestimated and the scale reader does not recognize that one or more annuli are obliterated.

Errors also result if the amount of resorption is overestimated (see section on "Confirmation of Year Marks"). This misjudgment usually occurs when scale readers conclude that a partially resorbed annual ring at the scale margin indicates that all of the marginal growth of the current year was resorbed. The resorbed annulus is included in the age determination. If resorption has been slight, however, the retarded growth at the scale margin represents growth that occurred late in the current year. The "resorbed annulus" should not be included in the age determination. We suggest that if scales with evidence of resorption at the margin must be used, they should show some new growth at the scale margin.

SUMMARY AND CONCLUSIONS

Most annuli or boundaries between the annual fields of growth on scales of chum salmon are of two main types. The first type is a circulus that is poorly formed, faint, and fragmented. The circulus is usually "cut over" by the first circulus of new growth. The annual ring usually is in conjunction with the annulus of type 1, but sometimes is not apparent. The second type of annulus is a circulus of "normal" appearance in the annual ring. If the width and spacing of the circuli of the annual ring are similar, the annulus is the last circulus of the ring preceding the first circulus of new growth. If a change in the rate of scale growth is reflected within the annual ring, the annulus is the narrowest circulus bracketed by the narrowest interspaces in the annual ring. The position of the annulus varies relative to the annual ring. Examples show the annulus centrally located in the ring and at the anterior and posterior margins.

Direct evidence that annuli are recognizable age indices was obtained from scales of marked chum salmon; an average of 98% (range 96–100) of the age determinations of three scale readers agreed with the known ages of the fish. The time of annulus formation and the start of new growth extends from as early as March to the end of June and possibly to the end of July. The long interval in which new growth starts causes problems in distinguishing marginal growth of the current and previous years. Information on the rate of new growth can sometimes aid in distinguishing growth of the current and previous years and the presence of an annual ring at the scale margin early in the season may indicate that marginal growth is of the previous year. The annual ring begins to form as early as August on scales of some chum salmon but does not appear on the scales of others until new growth begins, which may be as late as July of the next year. Scale growth may be such that no annual ring is detectable.

Age determination from 610 scales of a single chum salmon provided evidence in support of the assumption that all readable scales have the same number of annuli. Modification of the growth of scales adjacent to large areas of regeneration may be a main cause of supplementary checks. Age determinations from scales that give evidence of resorption are also subject to error. The main error detected was due to overestimation of the amount of resorption.

ACKNOWLEDGMENTS

We thank Dr Ted S. Y. Koo of the University of Maryland and Mr H. T. Bilton and Dr M. P. Shepard of the Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C., for their constructive criticism.

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Additional Comments on the Genus *Anonyx* (Crustacea: Amphipoda) of the Atlantic and Arctic Coasts of North America[1]

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Steele, D. H. 1969. *Additional comments on the genus Anonyx (Crustacea: Amphipoda) of the Atlantic and arctic coasts of North America.* J. Fish. Res. Bd. Canada 26: 683–686.

Recent examination of type specimens at the Zoological Institute in Leningrad has shown that a previous identification of *Anonyx pacificus* Gurjanova for the northwest Atlantic is changed to *A. makarovi* Gurjanova. *Anonyx pacificus* Gurjanova (in part) and *A. kurilicus* are considered to be synonyms of *A. nugax*. Other problems concerning the taxonomy of the eight northwest Atlantic species of *Anonyx* are discussed.

Steele, D. H. 1969. *Additional comments on the genus Anonyx (Crustacea: Amphipoda) of the Atlantic and arctic coasts of North America.* J. Fish. Res. Bd. Canada 26: 683–686.

L'examen de spécimens-types, principalement à l'Institut de Zoologie de Léningrad, a montré que *Anonyx pacificus* Gurjanova, rapporté récemment pour l'Atlantique nord-occidental, doit être ré-identifié comme étant *A. makarovi* Gurjanova. *Anonyx pacificus* Gurjanova (en partie) et *A. kurilicus* Gurjanova sont synonymes de *A. nugax*. D'autres questions relatives à la taxonomie des huit espèces d'*Anonyx* de l'Atlantique nord-occidental sont discutées.

Received November 4, 1968

SINCE THE PUBLICATION of the account on the genus *Anonyx* in this area (Steele and Brunel, 1968) I have had the opportunity to study collections of *Anonyx* in the Zoological Institute of Leningrad, where it has been possible to examine the types of the species and subspecies described by Gurjanova (1962). As a result it was found that one of our previous determinations was in error. In addition, it is now possible to comment on Gurjanova's species more accurately. Only the eight species of the preceding paper are discussed here; those that are confined to the Pacific will be considered at a later date.

Some of the old type specimens of Stimpson and Bate, recently discovered in the British Museum of Natural History, have also been examined and reclassified.

Anonyx nugax (Phipps, 1774)

NEW SYNONYMY

Anonyx nugax pacificus (part) — Gurjanova, 1962, p. 219–225, fig. 68A, B (not fig. 69A, B).
Anonyx kurilicus Gurjanova, 1962, p. 242–244, fig. 78.

As discussed previously (Steele and Brunel, 1968), Gurjanova (1962) has described considerable variation in this species. However, after examining

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[1] Studies in biology 122 from Memorial University of Newfoundland, St. John's, Nfld.

Printed in Canada

specimens from its entire circumpolar range, including many from the Zoological Institute in Leningrad, I am unable to discern the differences mentioned by Gurjanova between specimens from the Siberian seas and those collected elsewhere (Table II in Steele and Brunel, 1968). The size of the eye varies with the state of preservation, sex or maturity, or both, of the specimen. The palm of peraeopod 1 may be either concave or straight. The seta in front of the blunt spine on peraeopods 3 and 4 shown by Gurjanova (1962) is apparently an artifact as I have never found it on any specimen, including the slide preparations of the Zoological Institute. Contrary to the assertion of Gurjanova, specimens from Siberian seas do have setae on the lateral plate of the third metasome segment. The largest specimen that I found in the Zoological Institute (all were not examined) was only 45 mm long. Measurements of the proportions of the second antenna peduncle and of peraeopod 5 that I have made are similar throughout the range of the species. Thus the distinguishing features of Siberian specimens described by Gurjanova do not appear to be reliable.

Nevertheless, the specimens collected in the area extending from the European Arctic to the Laptev Sea differ from those found elsewhere in that the spine on the constriction of uropod 2 is relatively long. Measurements made on specimens from the entire circumpolar range of the species will be presented in detail later.

Examination of the syntypes of *Anonyx nugax pacificus* from the Sea of Japan showed them to be typical *A. nugax*. (The collection also includes a number of specimens of an undescribed species of *Anonyx* closely allied to *Anonyx eous* Gurjanova.) Therefore this subspecies has no validity. However, the specimen from the Okhotsk Sea figured by Gurjanova (1962) which was reexamined, was found to be a distinct undescribed species closely allied to *A. nugax*. It will be described subsequently.

On the other hand, the specimens that we identified as *A. pacificus* Gurjanova are in fact *A. makarovi* Gurjanova. The type specimen of the latter is a young animal (approximately 18 mm long) but readily identifiable with our specimens. It should be emphasized, however, that Pacific specimens of this species often do not have a well-defined constriction on uropod 2, that the constriction is more distally situated and the spine often not much longer than the proximal spines, as is the case with the type described by Gurjanova.

Anonyx kurilicus Gurjanova is also a synonym of *A. nugax*. The type is a small immature specimen approximately 10 mm long. Although the upper lip is small and the constriction on uropod 2 is slight, it is otherwise a typical young *A. nugax*. The rami of uropod 3 are not nearly as narrow as figured by Gurjanova.

Anonyx laticoxae Gurjanova, 1962

The type (male, mature with calceoli) from the Sea of Okhotsk (50° 53′N, 157°28′2″E) agrees well with the description and figures presented in Steele and Brunel (1968).

Anonyx ochoticus Gurjanova, 1962

The two type specimens of this species (designated as cotypes) belong to two distinct species. The one on which the description and figures of Gurjanova (1962) were apparently based is similar to the form described in Steele and Brunel (1968) under that name. It has the straight dorsal profile on the keel of the urosome segment 1 and the constricted uropod 2 with the long spine (since the slide preparation is on its side, it could not be determined whether the uropod was completely constricted). Moreover, many of the apparent discrepancies between the two descriptions are not found on the specimens. Thus the upper lip is more rounded, the palp of the first maxilla has more teeth, the outer plate of the maxilliped is rounded, and the side plate of peraeopod 1 is concave and slightly produced anteriorly, rather than as figured by Gurjanova.

The other cotype is apparently an undescribed species of *Anonyx*. It differs in that the inner ramus of uropod 2 is not constricted, both rami of uropod 2 are long and narrow without spines, the lateral plate of the third metasome segment is produced into a prominent upward projecting point, and the first urosome segment, although it does overhang the second, has a concave outline.

Anonyx debruyni Hoek, 1882

Examination of the two specimens from the Kara Sea described and figured by Gurjanova (1962) confirms them both to be *Anonyx debruyni*. The female corresponds to the description and figures in Steele and Brunel (1968). The male differs in the position of the constriction and armature of uropod 2 and the shape of the palm of peraeopod 2 which may be related to its unusually large size (approximately 23 mm long). It is the only specimen in the collections of the Zoological Institute which has these characters, but one or the other was seen on some of the other large animals. It appears, therefore, that they may be present on large specimens in various combinations.

On the other hand, some of the other characters mentioned by Gurjanova were not apparent to me on the specimens. Thus the lateral plate of metasome segment 2 is quadrate rather than rounded, the first urosome segment has flattened areas on either side of a small central keel rather than three keels, and the ventral lobe on the second segment of peraeopod 7 is not prominent.

As suspected, *A. debruyni orientalis* is a distinct species, distinguished by its small upper lip, unconstricted uropod 2 armed with numerous short spines, and by the inner ramus of uropod 3 which is setose on both margins.

On the other hand, *A. knipowitchi* seems to be the representative of *A. debruyni* in the Pacific rather than *A. orientalis*. It is very similar to *A. debruyni* and differs only in the straight, defined palm of peraeopod 1 and the less produced upper lip. The latter, however, is more produced and more rounded than as figured by Gurjanova.

Anonyx compactus Gurjanova, 1962

The specimens in the Zoological Institute agree well with the figures and descriptions in Steele and Brunel (1968), and the deviations between these and Gurjanova's were not apparent in the specimens. Thus the upper lip although small is more prominent than figured by Gurjanova, the first coxal plate is concave anteriorly, the tooth on peraeopod 1 is not divergent, and the dorsal notch on the first urosome segment is not so deep.

The following recently discovered type specimens were examined in the British Museum of Natural History.

Anonyx exiguus Stimpson 1853. No. 68: 107(28). Off Cheney's Head, Grand Manan, 1 specimen. This is a specimen of *Hippomedon serratus* described by Holmes (1905) and is a *nomen oblitum* according to the International Code of Zoological Nomenclature (1961).

Anonyx annulatus Bate 1862. No. 68: 107(13). Japan, W. Stimpson coll., 7 specimens. These are specimens of *Orchomenella*.

Anonyx punctatus Bate 1862. No. 68: 107(14). Bering Strait, W. Stimpson coll., 1 specimen. This is a specimen of *Onisimus*.

Since the genera to which both of these species belong are in need of revision, I will not attempt to refer them to current species. They are best left as *nomina dubia* (W. E. China personal communication).

Anonyx nobilis Stimpson 1853. No. 68: 107(23). Nantuckett Island, Mass., 2 specimens. No. 68: 107(9). Nantuckett Island, Mass., 3 specimens. These agree with the descriptions and figures of Shoemaker (1930) of *Tmetonyx nobilis* (Stimpson).

ACKNOWLEDGMENTS

Examination of the specimens in Leningrad and London was made possible through an NRC travelling grant and with the assistance of Memorial University. I would like to thank Academician Dr B. Bychowsky and Dr E. F. Gurjanova and the staff of the Zoological Institute (Leningrad), and Dr A. L. Rice and the staff of the Malacostraca Section of the British Museum (Natural History) (London) for their help during my visits to their respective institutions. Dr Pierre Brunel read the manuscript and provided the Résumé, and Dr W. E. China, Acting Secretary of the International Commission on Zoological Nomenclature, has commented on the status of the old type specimens.

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Age and Vision as Factors in Bottom Colour Selection by Rainbow Trout, *Salmo gairdneri*

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KWAIN, WEN-HWA, AND HUGH R. MACCRIMMON. 1969. *Age and vision as factors in bottom colour selection by rainbow trout, Salmo gairdneri.* J. Fish. Res. Bd. Canada 26: 687–693.

Rainbow trout exposed in a circular tank to a choice of black or white bottom at a light intensity of 10^{-2} lux were randomly distributed until the age of 14 months at which time a significant preference for black began and became more pronounced with increasing age.

Groups of fish (18–24 months of age) with normal eyes, without eye lenses, and lacking eyes, were held in total darkness and at 10^{-2}, 10, and 200 lux. In total darkness all groups were randomly distributed and quiescent. Fish without eye lenses selected black at all visible light intensities and acted similarly to normal fish at 10^{-2} lux. Fish lacking eyes were randomly distributed and more-or-less inactive at all intensities.

The eye is essential for bottom colour discrimination and behavioural patterns occurring in normal trout exposed to different light intensities.

Received October 10, 1968

INTRODUCTION

PRELIMINARY LABORATORY OBSERVATIONS on the behaviour of rainbow trout, *Salmo gairdneri* Richardson, established differences between fingerling and yearling fish with respect to light intensity (McCrimmon and Kwain, 1966; Kwain and McCrimmon, 1967). Young-of-the-year fish showed no preference when offered a choice of black or white bottom under a series of test light intensities. Older fish, however, demonstrated a highly significant preference for black at a low intensity of 10^{-2} lux, but less preference with increasing light intensity.

The present set of experiments was designed primarily to establish more precisely at what age bottom colour preference becomes significant in the ontogeny of rainbow trout. All observations were made at the low light intensity of 10^{-2} lux because of the optimum response at that level of light.

Any response to light intensity and bottom colouration, as evidenced in older rainbow trout, obviously requires the use of one or more receptor organs by the fish. Receptors known to be light-sensitive among fishes include the eye, the pineal organ, the midbrain, and dermal cells (Breder and Rasquin, 1947, 1950; Rasquin, 1958; Steven, 1963; Hafeez and Ford, 1967). In order to assess the importance of the eye as a photoreceptor, a comparison was made

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between normal yearling trout and others from which the eye lenses had been removed, or the eyes had been excised.

MATERIALS AND METHODS

Hatchery-reared rainbow trout were used throughout the present study. In order to avoid diurnal rhythm (Ali, 1961), a continuous light intensity of 50 lux was provided at the water surface.

The circular tank and experimental procedure were as described by Kwain and McCrimmon (1967). The bottom of the tank was divided equally into eight sectors, each alternately painted black or white. Observations on normal fish were made at a light intensity of 10^{-2} lux, measured by an A-3 supersensitive darkroom meter (Science and Mechanics). Fish were tested at monthly intervals to an age of 30 months.

Differences in behaviour between intact trout and those from which eye lenses or eyes had been removed were observed at test light intensities of total darkness, 10^{-2}, 10, and 200 lux. Eye lenses were removed without damage to other tissues by means of forceps after simply cutting a small slit on the cornea. Eyes were excised after the end of the optic tract was cut. Before both operations the fish were anaesthetized in a solution of M.S. 222, and allowed to recover in a holding tank for at least 2 weeks before being used experimentally.

All data were obtained by means of time lapse photography, with either an Exacta 35 mm or an Euring movie camera. Data were analyzed using the Chi-square test and the results were corrected by combined probabilities from the tests of significance (Fisher, 1954).

RESULTS

AGE AND BOTTOM COLOUR PREFERENCE

Among normal rainbow trout tested at monthly intervals from the time of complete absorption of the yolk sac to the age of 30 months, no statistically significant preference for either black or white bottom occurred until an age of 14 months, at the test intensity of 10^{-2} lux (Table 1).

However, visual observation suggested that a preference for the black bottom was developing during the previous 4 or 5 months, a contention which would seem to be supported by the tabularized data. Preference for the black bottom after 14 months continued to be significant and became more pronounced with age.

VISION AND BOTTOM COLOUR PREFERENCE

Observations on the response of groups of normal fish, fish with eye lenses removed, and fish with eyes excised showed differences between groups and between light intensities except when held in total darkness (Table 2). In total darkness (Fig. 1*a*), fish of all groups remained almost stationary and were randomly distributed over the bottom of the tank.

Normal fish (i.e., fish with eyes intact), when exposed to 10^{-2} lux (Fig. 1*b*), showed a decided preference for black ($P < 0.005$), swam slowly if at all, and appeared to be under no obvious stress. The fish became increasingly active at the higher light intensities of 10 lux (Fig. 1*c*) and 200 lux (Fig. 1*d*). At the latter intensity, a school was formed (Shaw, 1961) with the fish swimming collectively in either a clockwise or a counterclockwise direction around the

TABLE 1. Influence of age on distribution of rainbow trout on white and black bottom of experimental tank when exposed to a light intensity of 10^{-2} lux. Data are the means of 20 replications with 20 fish each.

Age (*months*)	No. fish	No. fish at each location White bottom	 Black bottom	*P*
1	20	9.90	10.10	0.89
2	20	9.35	10.65	0.80
3	20	10.25	9.75	0.78
4	20	9.15	10.85	0.92
5	20	9.35	10.65	0.30
6	20	8.95	11.05	0.35
7	20	10.75	9.25	0.37
8	20	11.50	8.50	0.70
9	20	9.15	10.85	0.45
10	20	8.60	11.40	0.30
11	20	9.65	10.35	0.54
12	20	9.00	11.00	0.45
13	20	8.05	11.95	0.20
14	20	5.35	14.64	0.01[a]
22	20	4.50	15.50	0.002[a]
30	20	3.85	16.15	0.001[a]

[a] Significant at 0.05 level.

TABLE 2. Influence of light on distribution of three groups of rainbow trout in the selection of black and white bottom. Data based on 20 replications with 20 fish each.

Light intensity (*lux*)		Selection of black bottom Normal	 Lenses removed	 Eyes excised
0	$\overline{X}$	11.00	11.00	9.80
	%	55.00	55.00	49.00
	χ^2	0.20	0.20	0.008
	P	0.70	0.70	0.95
10^{-2}	$\overline{X}$	16.70	16.00	10.60
	%	83.50	80.00	53.00
	χ^2	8.987	7.200	0.072
	P	0.005[a]	0.008[a]	0.85
10	$\overline{X}$	10.80	17.40	10.00
	%	54.00	87.00	50.00
	χ^2	0.128	10.952	0.000
	P	0.80	0.001[a]	0.999
200	$\overline{X}$	12.20	16.80	10.20
	%	61.00	84.00	51.00
	χ^2	0.968	9.248	0.008
	P	0.40	0.002[a]	0.95

[a] Significant at 0.05 level.

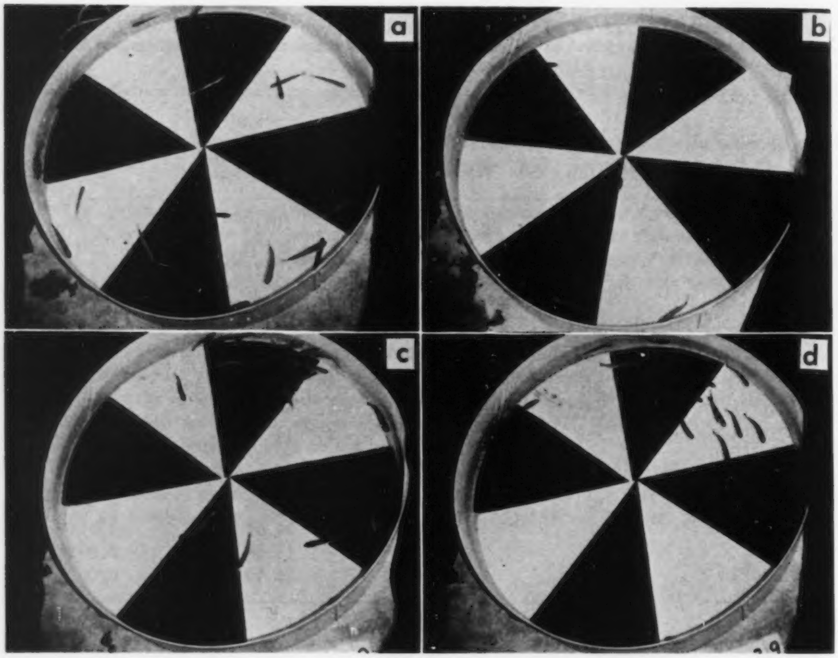

FIG. 1. Distribution of yearling rainbow trout over a black and white bottom when held (*a*) in total darkness, and when exposed to light intensities of (*b*) 10^{-2}, (*c*) 10, and (*d*) 200 lux.

tank. A significant preference for the black bottom did not occur at either the 10 or the 200 lux illumination.

Fish with lenses removed from both eyes showed a behaviour pattern at all the visible test light intensities similar to that of normal fish at 10^{-2} lux (Fig. 1*b*). Preference for the black bottom (Table 2) was statistically significant at each intensity ($P < 0.001$) and the fish displayed little inclination to swim actively. No tendency to school was apparent even at the highest test light intensity.

Fish with both eyes excised showed no preference for either black or white bottom at any of the test intensities (Table 2). Of interest was an instantaneous response, best described as a muscular contraction, which occurred on the sudden increase in light from a low to high intensity.

DISCUSSION

Previous studies on the response of rainbow trout to overhead light intensity (McCrimmon and Kwain, 1966) and bottom colouration (Kwain and McCrimmon, 1967) revealed a difference in behaviour between 5-month-old fingerlings and 20-month-old yearlings. Results of the present study not only confirm that there are differences in behavioural response between young-of-the-year and yearling fish, but establish that the change occurs statistically when the trout are 14 months of age.

In measuring this behavioural response to black and white bottom, there can be no assumption that the response is indicative of the ability or inability of the fish to perceive these visual stimuli. Although the work of Ali (1959) has shown that retinomotor responses increase with age, it is possible that fingerling trout may perceive visual stimuli but may lack a physiological or ecological urge to respond in the positive manner observed in older trout. Although the observed change in response has been related to age in the present analysis, it is possible that such behavioural changes may be conditioned by size of fish rather than its age and, if so, rate of growth would be a factor in establishing the timing.

From the observations on yearling trout with normal eyes and those without lenses or eyes, the importance of the eye in affecting the behaviour pattern and bottom colour selection is apparent. The response of normal fish at each test light intensity having been considered, two factors become apparent: there was an increase in swimming activity with increasing light intensity, and the selection of black bottom occurred only at the lowest level (10^{-2} lux) of visible light tested (Fig. 2). The failure of these fish to select black areas at the higher light intensities in significant numbers may be attributed

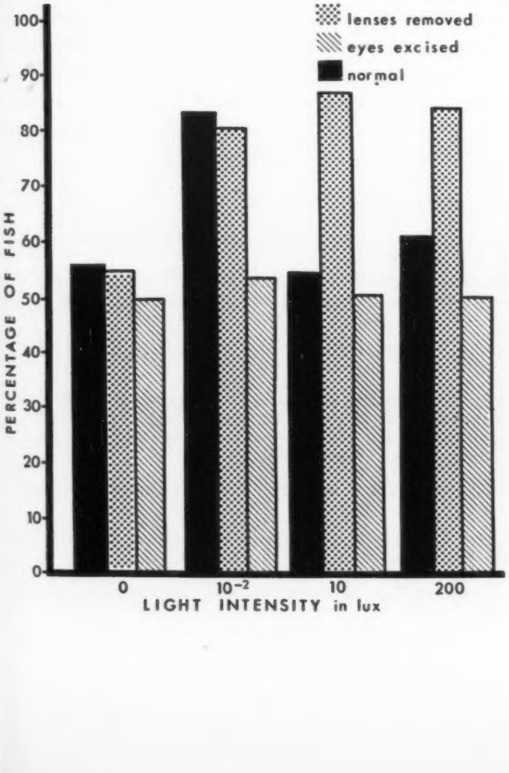

FIG. 2. Preference of yearling rainbow trout of three groups (normal, without eye lenses, and lacking eyes) for black bottom at four test light intensities.

either to the increased activity pattern or to a failure to distinguish black from white because of a desensitization of retinal photoreceptors by the passage of light through the lenses, or perhaps by a combination of both factors.

The fact that those fish without eye lenses selected the black bottom at all test light intensities (Fig. 2) tends to substantiate the suggestion that desensitization of the retinal receptors by bright light passing through the lenses may account for a failure of normal fish to differentiate black from white at other than low visible light intensities. As fish without eye lenses showed a statistical preference for black at all test light intensities, it is apparent that, without the lens, the retina or cut nerve endings still receive an adequate stimulus to discern black from white but not enough light to desensitize it. Also of interest is the fact that those fish without eye lenses maintained at all visible test light intensities the leisurely swimming pattern previously evidenced in normal fish only when held at 10^{-2} lux. The observation of Breder and Rasquin (1947) that the normally photonegative fish, *Astyanax mexican* (Fillipi), was still photonegative after the removal of eye lenses would seem to be a closely related phenomenon.

As eyeless trout exhibited a behavioural pattern at all test light intensities similar to normal fish in total darkness, the possibility can be ruled out that detection of differences in radiation, texture, or other factors between the black and white surfaces played a role in selection by normal or lensless fish. It would seem, also, that the eye is essential not only for colour discrimination but for receiving the light stimuli that affect swimming activity and general behaviour. The momentary response of blinded fish to sudden increases in light intensity, however, indicates that some photoreception is still possible.

The influence of light on the behaviour of rainbow trout is obviously complex. Further laboratory studies are required and should be supplemented by field observations on the ecological significance of behavioural patterns during ontogenesis of the species in its natural environment.

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Mass Mortalities and Behaviour of Brook Trout and Juvenile Atlantic Salmon in a Stream Polluted by Agricultural Pesticides

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After accidental spillage of the agricultural pesticides nabam and endrin into Mill River, Prince Edward Island, there were extensive mortalities among brook trout (*Salvelinus fontinalis* (Mitchill)) and juvenile Atlantic salmon (*Salmo salar* Linnaeus). Surviving trout and salmon showed abnormal behaviour including unseasonal downstream movements in summer and unusual response to an electric field. The abnormal behaviour could provide a useful biological indicator of pollution by the pesticides.

Received January 10, 1969

INTRODUCTION

Careless handling of agricultural pesticides has resulted in a number of severe fish kills in Prince Edward Island streams in recent years. Holden (1964) attributes most fish mortality arising from the use of agricultural chemicals, in Great Britain, to accidental spillage. The opportunity to observe the behaviour of brook trout (*Salvelinus fontinalis* (Mitchill)) and juvenile Atlantic salmon (*Salmo salar* Linnaeus) after exposure to agricultural pesticides was provided in Mill River in 1962 when a spray mixture containing the fungicide nabam (disodium ethylene bisdithiocarbamate) and endrin, a chlorinated hydrocarbon insecticide, was accidentally flushed from a potato sprayer into the upper reaches of the river, about 8.5 miles (14 km) above head of tide. The unusual behaviour observed could provide a useful biological indicator of stream pollution by the pesticides.

Mill River flows into Cascumpeque Bay on the north shore of Prince Edward Island. The drainage basin is about 18 square miles (47 km^2) in area. The upper reaches vary in width from a few feet near the source to 25 ft (7.5 m) at the head of tide. Maximum, minimum, and mean volume discharges in second-feet for the period October 1961 to September 1962 were 1050, 5.5, and 36.5 respectively.

OBSERVATIONS

Brook Trout near the Spillage Site

On August 5, the day after the spillage, there were about 200 dead trout at the spillage site; salmon do not occur in this part of the stream. Upstream

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trout were apparently healthy. No live trout was found in about 2 miles (3 km) of stream below the spillage site. Some pools contained over 300 dead trout. Down stream for the next mile there were dead and dying trout. In the shallower areas, trout swam to the surface, upright or on their sides. Some of these darted from time to time, either downstream or toward the bank. Those that reached the shore either shot out of the water and became stranded or moved convulsively until they were stranded. Similar convulsive movements and erratic swimming at the surface were noted by Kerswill and Edwards (1967) in young Atlantic salmon and brook trout in the Miramichi River, New Brunswick, after part of the drainage basin had been sprayed with DDT. They found that such behaviour of salmon and trout was a useful criterion of approaching death of caged specimens.

Some of the trout at the surface drifted downstream, with few swimming motions; a few swam steadily. When trout reached a pool they ceased swimming and most died there.

In the next several days, erratically swimming trout were common from about 4 miles (6 km) below the spillage site to at least 2.5 miles (4 km) above the head of tide, where remnants of a mill dam backs the water up slightly. Usually there is no salmon production above the obstruction.

By August 9, 4 days after spillage, no live trout was seen in the 6 miles (9.5 km) between the spillage site and the obstruction. On the same day, electrofishing at various points in the 6-mile stretch yielded only a few eels, *Anguilla rostrata* (LeSueur), and some sticklebacks, *Gasterosteus aculeatus* Linnaeus. Counts of dead trout in about 20 representative sections of the 6-mile stretch suggested that a total of 5000–8000 trout died. The total was probably much higher since dead trout became lodged in bottom debris and were difficult to find.

Brook Trout and Salmon Near the Head of Tide

On the morning of August 9, the 2.5-mile section between the old dam site and the head of tide was electrofished as part of an ecological study of the salmon and trout in Mill River. When exposed to the electric field in the water both species fell to the stream bottom, where they stayed and presumably died; eels and sticklebacks went to the anode. The response of trout and salmon was unusual since they normally swim rapidly to the anode at the voltage employed (245 d-c) until they are in the stunning part of the field (Saunders and Smith, 1954). They normally recover immediately when the electrode is removed from the water. The voltage was reduced to 200 but trout and salmon responded in the same way as before. Evidently the unusual response was due to exposure to the pesticides.

On the evening of August 9, dead and dying trout and salmon were observed about 1 mile (1.6 km) below the dam site, or 7 miles (11 km) below the spillage site. Counts were not made of dead fish in this part of the stream; some live fish were seen from the dam site to the head of tide.

On August 16, in the same part of the stream, many trout of all ages, and salmon fry and parr, were observed together in several deep pools. This was in marked contrast to the normal distribution of the two species in Ellerslie Brook, a similar small stream a few miles away (Saunders, 1960). Only rarely, in the small streams on Prince Edward Island, have trout and salmon been observed together in pools; young salmon are usually found in shallower, faster flowing areas. Another unusual feature was the presence of salmon near or at the surface of the pools. Usually juvenile salmon are close to the stream bottom (White, 1927).

Nearly all the fish in the pools were sluggish and were not disturbed when small pebbles were thrown among them. By August 20, after several rainy days, there were few fish in the pools. Some, as noted below, moved down into the estuary.

Movement into the Estuary

On August 12, after a slight increase in water flow, trout and salmon, including fish of the year (fry), were taken in a trap in a 2-way counting fence at the head of tide (Fig. 1). Normally brook trout (Smith and Saunders, 1958) and Atlantic salmon parr (Saunders, 1960) do not move to brackish water in summer, or salmon fry (Huntsman, 1945) except during freshets.

Mortalities among the fish in the counting fence trap were high. Of the 417 trout captured, 133 (32%) died shortly after entry into the trap; of the 944 salmon, 43 (5%). The salmon parr that died were invariably those that

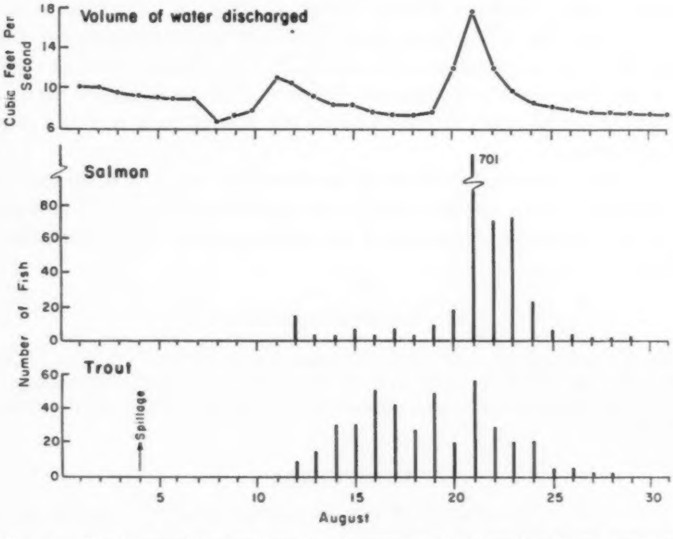

FIG. 1. Numbers of descending brook trout and Atlantic salmon trapped at the mouth of Mill River after spillage of pesticides on August 4.

displayed very white sides and undersurfaces when they entered the trap.

To check on possible delayed mortalities of descending fish, trout (28) and salmon parr (30) were removed from the trap on August 23 and placed in live-holding cages in the tidal area below the fence. Within 3 days, 19 (80%) of the trout were dead; 5 (16%) of the salmon died on August 24. There were no further deaths among the fish to their release on September 11.

There were trout and salmon in the lower reaches of Mill River when observations terminated in early October. These fish could have suffered above-normal mortalities during the next winter. Kerswill and Edwards (1967), Rudd (1964), and Ogilvie and Anderson (1965) observed that fish exposed to pesticides suffered heavy mortalities when later exposed to cold water.

OTHER SPECIES

No dead eels were observed. Sticklebacks were more resistant to the toxic effects of the pesticides than either trout or salmon. Deaths among sticklebacks were not evident until August 14; mortalities were moderate from then on.

DISCUSSION

Since two pesticides were present in Mill River, the specific toxic substance is not known. Endrin is known to be highly toxic to fish, nabam less so (Rudd and Genelly, 1956); whether they potentiate each other is not known.

Spillage of agricultural pesticides into streams with resulting extensive mortalities of fish is not unique to Mill River. I have examined three other streams on Prince Edward Island where spillage of agricultural pesticides resulted in heavy fish kills; there have been newspaper accounts of others.

Pesticides may spill into streams when the sprayers are filled at the streams, or later while they are being cleaned. In view of the toxicity of many agricultural pesticides to fish, only small amounts are needed to wipe out a population in a small stream.

To reiterate, aberrant swimming, gathering of trout and salmon in pools, unusual response to an electric field, and unseasonal downstream movements may be useful biological indicators of the presence of at least endrin or related insecticides.

ACKNOWLEDGMENTS

Field operations were under the immediate supervision of Mr Cyril Williams. The assistance of Miss Mary Holmes and Mr F. L. Swan in the laboratory is gratefully acknowledged. Stream flow data were provided by the Canada Department of Energy, Mines and Resources, Inland Waters Branch.

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NOTES

Mass Mortality of Estuarine Fauna at Bideford, P.E.I., Associated with Abnormally Low Salinities

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THOMAS, M. L. H., AND G. N. WHITE. 1969. *Mass mortality of estuarine fauna at Bideford, P.E.I., associated with abnormally low salinities.* J. Fish. Res. Bd. Canada 26: 701–704.

Spring thaw discharges large quantities of fresh water into estuaries in the Gulf of St. Lawrence. Surface freshwater layers of 1 m are normal but deeper water usually remains at close to full salinity. Shallow-water animals are adapted to withstand low salinities but those from deeper water are not. In May 1967 an up-estuary gale caused the buildup of an extraordinarily deep freshwater layer in Bideford River, P.E.I.; salinities at 3 m fell to less than 1‰. Scuba surveys after this phenomenon revealed extensive mortalities in a variety of species. Several of these species often occur in low-salinity areas and it is suggested that mortalities resulted from the very rapid salinity change combined with warming water temperatures.

Received October 21, 1968

WELL-DOCUMENTED ACCOUNTS of mass mortalities in the sea are rare. Brongersma-Sanders (1957) reviewed the literature, showing that changes in temperature or salinity, toxic phytoplankton blooms, and oxygen lack were the most frequently reported causes of such mortalities.

Large changes in salinity are, in general, confined to coastal waters, and mortalities ascribed to this cause are usually in bays or estuaries. Typical cases involving mortalities of oysters in Mississippi Sound associated with flood waters are described by Butler (1949, 1952).

In the Gulf of St. Lawrence area, large amounts of fresh water are discharged during the relatively short period of spring thaw. In sheltered locations the mixing of the runoff and sea water is slow, particularly if sea ice is still present. Surface freshwater layers over 1 m deep are normal in many estuaries at this season. Often a very sharp halocline is present, the underlying water being close to full salinity. Consequently, organisms such as *Mya arenaria*, the soft shell clam, and *Littorina saxatilis*, the northern rough periwinkle, which permanently inhabit the zone shallower than the halocline are exposed annually to fresh water and are adapted to these conditions. Other characteristic members

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of the shallow-water fauna, for example *Nassarius obsoletus*, the mud snail, migrate out of the zone seasonally, thus avoiding fresh water. Animals permanently inhabiting water deeper than the halocline may not normally encounter drastic salinity reductions.

Bideford River, P.E.I., is an estuary typical of this region. Ice cover generally lasts 4 months and maximum ice thicknesses of over 1 m are normal. During heavy runoff in the spring of 1967 an up-estuary gale caused melt water to build up an extraordinarily deep freshwater layer. This was followed by extensive mortalities of a variety of benthic species.

Vertical salinity profiles for the period May 5–17 taken at the Oyster Unit wharf, in 3 m of water, in one arm of Bideford River, are presented in Fig. 1. The profile for May 5 illustrates the sharp halocline associated with runoff, a typical situation for this season. On the night of May 7–8 a southeast gale occurred and apparently drove the surface layer up-estuary, completely replacing sea water to at least 3 m deep in the inner part of the estuary. The two profiles for 0930 and 1530 hr May 8 show the result. Salinities during this period were less than 1‰ from top to bottom. The profile for May 9 demonstrates return of water of over 25‰ salinity to the bottom and a curious double

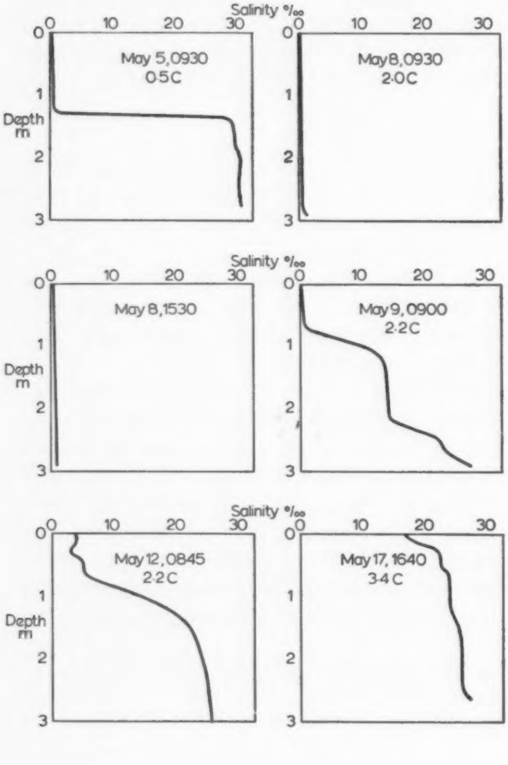

FIG. 1. Salinity profiles at the Oyster Unit wharf, Bideford River, P.E.I., May 5–17, 1967. Temperatures are daily means.

halocline in the overlying water. By May 17 a typical salinity regime was re-established. During this period, water temperatures rose steadily from a mean of 0.5 C on May 5 to 2.0 C on May 8 and to 3.4 C May 17. There was negligible thermal stratification.

After this phenomenon scuba surveys of the area were carried out to check on possible mortalities of the fauna. Epifaunal mortalities were estimated along transects and infauna were dug in several locations. Mortality of a variety of species was observed and no other possible cause than the reduced salinity was detected.

Anguilla rostrata, the American eel, showed virtually complete mortality where the freshwater layer extended to the bottom. Counts indicated an average of one dead eel per square meter. Eels overwinter in burrows in the mud in this area and many of those dead were still partially buried. The only other dead fish observed was a single specimen of *Tautoglabrus adspersus*, the cunner. *Asterias vulgaris*, the common starfish, which was abundant in some areas, suffered complete mortality where fresh water reached the bottom. Among the pelecypod molluscs, extensive mortalities were observed in *Macoma balthica*, *Tellina agilis*, and *Yoldia limatula*, and slight mortalities were observed in *Mytilus edulis*, the blue mussel. A predatory gastropod, *Lunatia heros*, the moon snail, was killed in shallow locations. Some specimens of the lobster *Homarus americanus*, which overwinters in burrows in the estuary (Thomas, 1968), were observed dead in their burrows. However, the main concentration of overwintering lobsters was down-estuary of the area where mortalities occurred. Some dead polychaete worms were observed but their rapid decomposition prevented specific identifications.

Subsequent grab sampling in the area showed large numbers of newly dead shells of *M. balthica* in two localities and few live specimens.

Mortalities of species such as *A. vulgaris* and *H. americanus* which cannot survive drastic salinity reductions (McLeese, 1956; Krogh, 1939) were not surprising. Species such as *Y. limatula*, *T. agilis*, and *L. heros*, which also suffered mortalities, do not normally inhabit low-salinity areas and are presumably unable to withstand fresh water. However, two of the species with the most extensive mortalities, *A. rostrata* and *M. balthica*, are typical of brackish waters in this area and their mortalities are hard to explain. *Anguilla rostrata* may inhabit either fresh or salt water during the "yellow" stage in which it is most frequently found in Bideford River. During the elver stage, eels can withstand abrupt and large salinity changes (Black, 1957). *Macoma balthica* is common in areas of sustained low salinities down to 2‰ (Lassig, 1956) and is locally common in areas where salinities are even lower than this in spring. Another bivalve, *Mya arenaria*, the soft shell clam, is common in the estuary but according to Lassig (1965) it does not occur where salinities are consistently lower than 4.5‰. In this respect it does not appear to be adapted to as low salinities as *M. balthica*, but it suffered no apparent mortality in the areas we checked. R.E. Drinnan (personal communication) did observe some mortality of *M. arenaria* in an adjacent area at this time.

It seems likely that the rapid change from 30 to less than 1‰ salinity did not allow needed acclimation in some species. The rising temperature during the period may also have contributed to mortality by increasing activity of species and thus their contact with the fresh water.

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Nucleotides and Related Compounds in Canned Shrimp

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Preliminary findings indicate that, although inosine-5′-monophosphate (IMP) has been reported to be fairly heat-stable, only 40% of IMP, 33.5% of adenosine-5′-monophosphate (AMP), and 25% of hypoxanthine remain in canned shrimp. Heat destruction can account for the reduced levels except for hypoxanthine. IMP predominates over AMP in Indian shrimp (*Metapenaeus dobsoni*), and hypoxanthine is also prominent in fresh shrimp. A significant reduction apparently occurs in the level of flavour components in canned shrimp. Small amounts of adenosine were detected in canned commercial samples.

Received August 19, 1968

Although much work has been reported in recent years on the role of nucleotides and related compounds as flavour components in fish, changes during ice storage alone have received the main attention as compared with other methods of processing like canning, except for a recent study (Mouri et al., 1968). Although existing knowledge is confined to fish, knowledge of shellfish and other invertebrates is increasing (Saito et al., 1958; Arai, 1966). Adenosine-5′-monophosphate (AMP) has been shown to be a flavour enhancer (Hashimoto, 1964). In view of the economic importance of canned shrimp exported from India in recent years, investigations have been made on the effect of canning on flavour components. Hypoxanthine alone has been studied in canned herring by Hughes and Jones (1966) to serve as an index of raw material quality.

Fresh shrimp from the Arabian sea (*Metapenaeus dobsoni*), the major commercial species, stored in ice overnight were employed for the study. After removing the head and shell portions, the samples were deveined and blanched in 5% brine for 10 min, 3½-oz portions were placed in 4-oz meat cans, hot 3.5% brine containing 0.2% citric acid was poured in, and the cans were exhausted for 15 min in steam before seaming. The cans were processed at 15 lb/in^2 for 30 min. The procedure described by Jones and Murray (1960) was adopted for extraction of the purine compounds and two-dimensional paper chromatography with the solvents, *n*-butanol:isobutyric acid:ammonia (20:10:1) (modified Löfgren solvent) and saturated ammonium sulphate:isopropanol:water (79:2:19) was employed for separation (Block et al., 1955). The first solvent leaves the nucleotides at the base line, and separates the nucleosides from the bases in a satisfactory manner. After identification under an ultraviolet lamp, quantitative estimation was made by elution with 0.1 N HCl. Molar extinction coefficients and absorption maxima given in Block et al. (1955) were employed for calculation.

It may be observed from the results that inosine-5′-monophosphate (IMP) remains the main constituent in Indian shrimp species studied, although AMP is also present in large amounts. The nucleotides and related compounds in canned shrimp (μm/g) are as follow:

Compounds	Fresh shrimp (as landed)	After canning in laboratory	Commercial samples			
			1	2	3	4
Adenosine-5′-monophosphate	1.40	0.47	0.18	0.16	0.36	–
Inosine-5′-monophosphate	2.75	1.10	0.23	0.22	0.65	–
Inosine	1.30	0.53	0.33	1.00	0.15	0.10
Adenosine	0	0	0.19	0.21	0.08	0.13
Hypoxanthine	2.09	0.53	0.24	0.43	0.18	0.12

Another finding is the presence of hypoxanthine even in fresh shrimp, although Tarr and Comer (1965) found little of it in Canadian pink shrimp (*Pandalus borealis*) and suggested that degradation of inosine is incomplete in shrimp. Examination of the sample after canning reveals that the residual level of the flavour components is only 25–40% of the concentration in the raw material. Although IMP is believed to be fairly heat-stable, detailed information is lacking on the heat stability of IMP and related compounds at higher temperatures employed in canning. With "Ribotide," a mixture of

IMP and GMP (guanosine-5′monophosphate) 86% recovery is reported at 115 C for 25 min (Product Data — Takada U.S.A. Inc.). In view of the significant reduction observed during canning even in the experimental samples, recovery experiments were conducted with IMP, AMP, and hypoxanthine to study the effect of heat processing for 30 min at 15 lb/in^2 (121 C). It was found that 60% of IMP, 42% of AMP, and 90% of hypoxanthine remained after heat treatment at 121 C. Since the percentages remaining in the canned shrimp were 40.1%, and 33.5%, and 25.4% respectively, it is concluded that heat destruction can account for the reduced levels in the canned product except in the case of hypoxanthine, where loss due to leaching may perhaps be equally significant. Further work is in progress on the exact mechanism. Moreover, Mouri et al. (1968) have observed that boiling may release AMP from ATP. Initial ATP level is, however, quite low in Indian fish and shellfish (Rajendranathan Nair and Bose, 1965).

One of the unusual features of this study is the presence of adenosine in commercial samples of canned shrimp. It is believed that adenosine does not accumulate in the muscle, since Saito et al. (1958) have postulated that deamination of AMP is accomplished indirectly in invertebrates like squids by a combination of 5′-nucleotidase and adenosine deaminase activity, the latter enzyme acting rapidly in crude extracts of squid muscle. Since adenosine is absent in the laboratory samples, both in fresh and canned condition, its origin is obscure. Adenosine was identified not only by comparison with standards using additional solvents but also by absorption ratios, 250/260 and 280/260 mμ.

It may therefore be noted from this study that there occurs a significant reduction in the level of flavour components like AMP and IMP during canning. Presence of larger amounts of hypoxanthine in fresh shrimp, and also the possible occurrence of adenosine in canned shrimp, need further investigation.

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Two Modified Stains for Use in Oyster Pathology

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This note describes two modified staining procedures for use in oyster pathology. One is a cresyl-fast violet stain for differentiating bacteria and fungi from tissue components in oysters. The other is a trichrome stain for collagen and bacteria in oyster tissue sections.

Received August 13, 1968

ONLY RECENTLY have a few special histological staining methods been developed for use in oyster pathology work (Farley, 1965; Pauley and Maulsby, 1967). Although many specialized staining techniques exist for detecting pathogens in vertebrate tissues, oyster pathologists have made little use of them. One reason for this is the tendency of cytoplasmic dyes to overstain oyster tissues, making it time-consuming to obtain a staining procedure which will consistently yield preparations of satisfactory quality. The two staining methods presented in this report will aid oyster pathologists to quickly identify certain pathogens and cell types that cannot be readily detected with routine hematoxylin and eosin stains.

Cresyl-fast violet stain — According to Puchtler and Sweat (1964), cresyl-fast violet stain is effective in differentiating bacteria and fungi from tissue components in human autopsy sections. However, this staining method is unsatisfactory for oyster tissue because of the strong affinity of oyster cell cytoplasm for cresyl-fast violet dye. A modified staining procedure for oyster tissue is as follows.

Fix the tissue in ice-cold solution of 15% formalin–calcium, as described by Pauley and Clarke (1967). Embed in Paraplast[3] and cut sections at 6–8 microns. Stain in cresyl-fast violet:

Cresyl fast violet	5.0 gm
Distilled water	500.0 ml
Glacial acetic acid	0.5 ml

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[3] Paraplast may be obtained from Aloe Scientific Supply Company, Seattle, Washington, USA.

Printed in Canada

The *p*H of the staining solution should be 3.7. Allow solution to stand for 16–20 hr before use. Do not filter.

The staining procedure is as follows. Clear in xylene, 2 changes for 3 min each. Rinse in 100, 95, 70, 50% ethanol for 1 min each and in tap water for 2 min. Stain for 10-20 sec in cresyl-fast violet solution. Wash in running tap water for 5 min. Drain well and remove excess moisture. Rinse in 50, 70, 95% ethanol for 1 min each and 2 changes of 100% ethanol for 10-15 sec each. Then clear in xylene, 2 changes for 3 min each. Mount in Technicon mounting medium.

The results are: bacteria — dark blue; fungi — blue or purple; cell nuclei — dark blue; cartilage — pink to red; mucous glands — pink to red.

This stain is not as good for distinguishing bacteria as the modified MacCallum–Goodpasture stain described by Pauley and Maulsby (1967), but facilitates the observation of both bacteria and fungi in the same oyster tissue. Bacteria and fungi appear vividly against a light blue background after differentiation. The four rinses in ethanol after staining provide differentiation by reducing the overstaining which occurs in oyster tissue, even after the short staining time. Cresyl violet acetate dye stains in a similar manner, but is not as satisfactory as cresyl fast violet.

Barbeito–Lopez trichrome stain — A second stain found useful for studies in oyster pathology is a modification of the Barbeito–Lopez trichrome stain (Lopez, 1946). The modified procedure is as follows.

Fix tissue in an ice-cold solution of 15% formalin–calcium, as described by Pauley and Clarke (1967). Embed in Paraplast, and cut sections of 6–8 microns. The staining solutions are:

Acetic formalin		
	Formaldehyde, 37–40%	4.0 ml
	Glacial acetic acid	0.2 ml
	Distilled water	100.0 ml
Acetic fuchsin		
	Ziehl's fuchsin solution[4]	10.0 ml
	Glacial acetic acid	0.2 ml
	Distilled water	100.0 ml
Aniline blue–orange G		
	Aniline blue (water soluble)	0.5 g
	Orange G	2.0 g
	Phosphotungstic acid	1.0 g
	Distilled water	100.0 ml

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[4] Ziehl's fuchsin may be made in the following manner: basic fuchsin (1.0 g); phenol (5.0 g); ethanol, 90% (10.0 ml); distilled water (100.0 ml). Grind the fuchsin with phenol in a mortar. When the dye is crushed, add the alcohol in 10 successive lots and continue grinding. Then use water in 10 successive lots to wash out the mortar. Filter the washings. Age for 30 days for consistent staining results. (This method of preparing the Ziehl's fuchsin was kindly given to us by Virginia A. Liddell, Bureau of Commercial Fisheries Laboratory, Oxford, Maryland, in a personal communication, 1966.)

The staining procedure is as follows. Clear in xylene, 2 changes for 3 min each. Rinse in 100, 95, 70, 50% ethanol for 1 min each and in running tap water for 5 min. Stain in acetic formalin for 1 min and rinse in tap water, two quick dips; in 95% ethanol for 45 sec; and in 100% ethanol, 2 changes for 1½ min each. Clear in xylene, 2 changes for 3 min each. Mount in Technicon mounting medium.

The results are: bacteria — red; mucus glands — orange; Leydig cell cytoplasm — pale orange; cell nuclei — violet; collagen — blue; cartilage — brillant blue; epithelial structures — violet; leucocytes — violet.

The aniline blue–methyl orange solution originally used by Lopez (1946) is replaced by the anilin blue–orange G solution used by Pauley (1967), because the original solution gives poor results on oyster tissue. The modified procedure provides excellent contrast, with the bacteria vividly distinct as in the modified MacCallum–Goodpasture stain (Pauley and Maulsby, 1967), and the collagen brillant blue as in the modified Mallory's stain (Pauley, 1967). Differentiation is done in the terminal ethanol rinses. This stain has the benefit of being a trichrome and a bacterial stain simultaneously.

Acknowledgments — This report is based on studies performed under Contract No. 14-17-0007-441 between the Pacific Northwest Laboratory and the United States Department of Interior, Bureau of Commercial Fisheries.

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First Record of Occurrence of the Northern Redbelly Dace, *Chrosomus eos*, within Prince Edward Island

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Four specimens of *Chrosomus eos* were collected from the Morell River, Kings County, Prince Edward Island. Its occurrence within the Province has not been previously recorded. The distribution of this species within the neighboring provinces is noted.

Received October 21, 1968

Printed in Canada

THE NORTHERN REDBELLY DACE, *Chrosomus eos* Cope, has not been previously reported within the province of Prince Edward Island. Its range extends from the Peace–Mackenzie system and Hudson Bay drainage south to a line from Colorado to Maryland. Within the Maritime Provinces of Canada, Livingstone (1952) found *Chrosomus eos* to occur in Nova Scotia "From Windsor, Hants County to Lake Ainslie on Cape Breton Island." Scott and Crossman (1959) record its New Brunswick distribution as "the Saint John River system as far north as Grand Falls, but not above; in the Meduxnekeag, Digdeguash, Magaguadavic and Petitcodiac rivers. It has been reported from the Miramichi River by McKenzie (1959). A single specimen was taken at Station 20, the only record for the St. Croix River system." Further details of its recorded range can be found in Hubbs and Lagler (1964).

On June 5, 1967, four specimens of *Chrosomus eos* were collected from a shoal of small fish observed in a headwater tributary of the Morell River, Kings County, Prince Edward Island, at a road crossing approximately 500 yards south of the Cardross School (46°16′N lat, 62°38′W long).

They were captured with a dipnet in approximately 18 inches of water by the author and Mr Clare Birch. Water quality information for the area of capture is not available due to a lack of reliable water analysis equipment. However, the surrounding area was boggy in nature with darkly stained water. The stream bottom varied from coarse gravel to detritus.

The fish were identified as *Chrosomus eos* by the author. This identification was verified by Dr E. J. Crossman, Curator, Department of Ichthyology and Herpetology, Royal Ontario Museum. One specimen is now in the collection of the Royal Ontario Museum.

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